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Review of the millipede family Haplodesmidae Cook, 1895, with descriptions of some new or poorly-known species (Diplopoda, Polydesmida)

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Abstract

The polydesmoid family Haplodesmidae Cook, 1895 is reviewed and shown to be a senior subjective synonym of the family Doratodesmidae Cook, 1896, syn. n. The Haplodesmidae therefore encompasses six genera and 30 recognizable species, all keyed here, including the following six new species: *Eutrichodesmus basalis* **sp. n.** and *E. armatocaudatus* **sp. n.** from Vietnam; *E. communicans* **sp. n.** from Vanuatu, Melanesia; and *E. latus* **sp. n.**, *E. similis* **sp. n.** and *E. incisus* **sp. n.** from China. The following new synonymies are proposed: *Prosopodesmus* Silvestri, 1910 = *Rhipidopeltis* Miyosi, 1958; *Doratodesmus* Cook *in* Cook & Collins, 1895 = *Pauroplus* Chamberlin, 1945, = *Eucondylodesmus* Miyosi, 1956, = *Scolopopyge* Hoffman, 1978, = *Selminarchus* Hoffman, 1978, = *Crenatidorsus* Zhang *in* Zhang & Wang, 1993; *Eutrichodesmus* Silvestri, 1910 = *Dimorphodesmus* Murakami, 1966, = *Ascetophacus* Hoffman, 1977, = *Cerastelachys* Hoffman,

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1977, = *Dyomerothrix* Hoffman, 1982, = *Parapauroplus* Zhang *in* Zhang & Wang, 1993, = *Pocillidorsus* Zhang *in* Zhang & Wang, 1993 (all syn. n.). The following new combinations are proposed: *Prosopodesmus sinuatus* (Miyosi, 1958), *Doratodesmus elegans* (Miyosi, 1956), *Doratodesmus grandifoliatus* (Zhang *in* Zhang & Wang, 1993), *Doratodesmus analdes* (Chamberlin, 1945), *Doratodesmus pholeter* (Hoffman, 1978), *Doratodesmus hispidus* (Hoffman, 1978), *Eutrichodesmus macclurei* (Hoffman, 1977), *Eutrichodesmus reclinatus* (Hoffman, 1977), *Eutrichodesmus cavernicola* (Sinclair, 1901), *Eutrichodesmus peculiaris* (Murakami, 1966), *Eutrichodesmus gremialis* (Hoffman, 1982), *Eutrichodesmus monodentus* (Zhang *in* Zhang & Wang, 1993), *Eutrichodesmus dorsiangulatus* (Zhang *in* Zhang & Wang, 1993) (all n. comb.).

Keywords
Diplopoda, Haplodesmidae, Doratodesmidae, taxonomy, synonymy, new species, cave, China, Vietnam, Vanuatu

Introduction

The millipede family Haplodesmidae Cook, 1895 has hitherto been considered a tiny group of the superfamily Polydesmoidea (Hoffman 1980) or, together with Doratodesmidae Cook, 1896, forming the superfamily Haplodesmoidea (Simonsen 1990). Haplodesmids encompass at least three small genera which are mainly characteristic of the southwest Pacific region (Hoffman 1980, 1982b; Simonsen 1990):

(1) *Cylindrodesmus* Pocock, 1889, with numerous junior synonyms and two unquestioned species (see review by Golovatch et al. 2001);
(2) *Helodesmus* Cook, 1896, also with a few synonyms and two species;
(3) *Prosopodesmus* Silvestri, 1910, with one junior synonym and again two species.

Hoffman (1980), with some reservations, also included therein the monotypic Japanese genus *Rhipidopeltis* Miyosi, 1958, which Simonsen (1990) ignored, but the latter added the broadly Australian genera *Agathodesmus* Silvestri, 1910, *Atopodesmus* Chamberlin, 1920 and *Atopogonus* Carl, 1926, apparently following Jeekel (1986). Both *Agathodesmus* and *Atopodesmus* are monotypic and their respective type species are *nomina inquirenda* known only from the female sex, whereas *Atopogonus* contains one species each in Australia and New Caledonia (Jeekel 1986).

Inasmuch as the status of *Inodesmus* Cook, 1896 (and of its type species, *I. jamaicensis* Cook, 1896, from a cave in Jamaica (Cook 1896b)) is unclear, it seems premature to formally consider it as a subjective senior synonym of *Atopogonus* (*cf.* Jeekel 1986; Hoffman 1999). Loomis (1975) provided an adequate description of what he identified as *I. jamaicensis* from a new cavernicolous sample from Jamaica, which does show strong resemblance to *Atopogonus* species (Jeekel 1986). Because the type material of *I. jamaicensis* is lost, the most reasonable solution would be to select a neotype, perhaps from among Loomis' material.

The current classification of Haplodesmidae, arranged in alphabetical order, is therefore as follows:

(1) *Agathodesmus steeli* Silvestri, 1910, the type species, briefly described without illustrations from a female from New South Wales, Australia (Silvestri 1910).
(2) *Atopodesmus parvus* Chamberlin, 1920, the type species, very succinctly described without illustrations from two females from Tasmania, Australia (Chamberlin 1920). New material, including males, that was recently redescribed as this species (Mesibov 2002) actually represents an *Asphalidesmus* Silvestri, 1910, a member of the Dalodesmoidea (Golovatch 2003). Thus, with the synonymy *Asphalidesmus* = *Atopodesmus* established by Mesibov (2002), *Atopodesmus* must be removed from Haplodesmidae.
(3) *Atopogonus baccatus* Carl, 1926, the type species, described and still known only from New Caledonia (Carl 1926).
(4) *Atopogonus bucculentus* Jeekel, 1986, described and still known only from Queensland, Australia (Jeekel 1986).
(5) *Cylindrodesmus hirsutus* Pocock, 1889, the type species, currently known to be distributed throughout the tropics (especially islands) and found in several European hothouses, with both bisexual and parthenogenetic populations (Golovatch et al. 2001).
(6) *Cylindrodesmus villosus* Pocock, 1898, described and still known only from Rotuma Island, Fiji (Golovatch et al. 2001).
(7) *Helodesmus parvulus* (Attems, 1930), first described as *Gonomastis parvula* Attems, 1930, from Sumatra, Indonesia, later transferred to *Helodesmus* by Hoffman (1964).
(8) *Helodesmus porosus* Cook, 1896, the type species, very poorly described from Java, Indonesia (Cook 1896c), but fortunately redescribed from near-topotypic samples under the name *Porauxus pangrangus* Chamberlin, 1945 (Chamberlin 1945), synonymized by Hoffman (1964).
(9) *Prosopodesmus jacobsoni* Silvestri, 1910, the type species, first described from Java, Indonesia (Silvestri 1910), now known to be pantropical (Hoffman 1999).
(10) *Prosopodesmus panporus* Blower & Rundle, 1980, described and still known only from the Royal Botanic Gardens, Kew, England. It is not yet known where this species occurs naturally (Blower and Rundle 1980).

With the addition of the following genus and species, as suggested by Hoffman (1980), we arrive at just a handful of mono- or oligotypic genera forming the Haplodesmidae:

(11) *Rhipidopeltis sinuata* Miyosi, 1958, the type species, described and still known only from Yamaguchi Prefecture, southern Honshu, Japan (Miyosi 1958).

Both Hoffman (1982a, 1982b) and Simonsen (1990) emphasized the close relationship between Haplodesmidae and Doratodesmidae, which is especially evident in gonopod conformation. Based on the presence of peculiar, bisegmented and apparently

tactile setae in the tergal trichome of *Cylindrodesmus* (the type genus of Haplodesmidae), and on one of the unquestioned doratodesmids he described, Hoffman (1982a: 91) surmised that "Possibly future investigations will discover additional specializations shared by various haplodesmid and doratodesmid species".

The basic characters considered to distinguish these families are as follows:

(1) Haplodesmidae are incapable of volvation, whereas Doratodesmidae are capable of conglobation due to conspicuously enlarged and laterally expanded paraterga 2 (Hoffman 1982a, 1982b);
(2) In Haplodesmidae, the gonopod coxae have only a few ventral setae, whereas in Doratodesmidae such setae are numerous (Simonsen 1990);
(3) Paraterga are either absent from body segment 3 onwards (Haplodesmidae) or present on all segments (Doratodesmidae) (Simonsen 1990); and
(4) Ozopores in Haplodesmidae are borne on special boletiform porosteles, or tubercles, whereas such porosteles are absent from Doratodesmidae (Hoffman 1982b; Simonsen 1990).

Based on the available descriptions, the body in Haplodesmidae is subcylindrical, the dorsum being especially strongly convex; the collum is usually large, sometimes flabellate, often covering the rear part of the head from above; the metaterga are conspicuously setose to very densely hirsute, often tuberculate (in *Prosopodesmus* and *Rhipidopeltis* very much like in Pyrgodesmidae Silvestri, 1896); the paraterga are usually nearly absent, with porosteles mostly but not always present; the pore formula is normal in most cases, with the ozopores lying laterally near the middle of the metaterga. The gonopods vary from very simple and uniramous, showing no traces of a microvillose pulvillus at the orifice of the seminal groove, to quite complex, bi- or triramous (sometimes with one of the branches being a flagelliform solenomere). Sometimes a solenomere branch is absent (*Prosopodesmus, Rhipidopeltis*), sometimes (*Prosopodesmus*) being replaced by a distinct microvillose pulvillus (= hairpad) at the orifice of the seminal groove in the distal one-third. The telopodite is sometimes strangely geniculate at about midway and devoid both of a coxal cannula and a seminal groove (*Atopogonus*). The gonocoxae have more than a few setae ventrally.

In contrast, the body of Doratodesmidae usually has bare or (less frequently) setigerous tubercles arranged in 2-3 transverse rows, often, but not always, with peculiar mid-dorsal crests or processes, which either increase or decrease in size towards the telson. The collum is usually small (apparently in negative correlation with the hypertrophied paraterga 2). The paraterga are always declivous, directed ventrolaterad, usually more or less strongly lobulate laterally and caudolaterally; paraterga 2 are mostly subvertical, greatly enlarged and rounded, often also lobulate ventrally and subventrally, with the volvation pattern (= overlap) only switching to typical from segment 5 (Golovatch 2003). The pore formula is usually normal, with most ozopores, when present, lying off or even at lateral margin of paraterga, close to the midway to somewhat off the caudal corner of paraterga, only seldom borne on small, inconspicuous

knobs resembling porosteles. The gonopods also range from rather simple to fairly complex, usually being elongate. The seminal groove usually shifts laterad at the end of the femorite to end either distally or (sub)apically; with or without pulvillus, only rarely is a solenomere branch present. The gonocoxae usually have abundant setation ventrally, only seldom with fewer setae.

Even from these brief characteristics, it is evident that none of those proposed by Simonsen (1990) as typical of Haplodesmidae is reliable. Indeed, the degree of variation in the number of ventral setae on the gonocoxae in Polydesmoidea is underestimated. For example, the few East Asian species of *Polydesmus* Latreille, 1803 (Polydesmidae), in contrast to their Euro-Mediterranean counterparts, show strongly setose gonopod coxae (Golovatch 1991). In addition, quite strongly developed paraterga are observed all along the body in *Prosopodesmus*, a genus formerly confused with typical genera of Pyrgodesmidae (e.g. Attems 1940). The same concerns *Rhipidopeltis*. Finally, porosteles of any kind are absent from *Atopogonus* and *Rhipidopeltis*, each ozopore opening in the middle of a smooth area (Miyosi 1958; Jeekel 1986).

We have recently obtained for study a disparate selection of species easily identifiable as Doratodesmidae, along with a few that looked more like Haplodesmidae or that bridged these groups. Having further examined the variation range of the structures they show, both peripheral and genitalic, we have arrived to the conclusion that the two families can be synonymized. The reasons for this will be given in detail in the Discussion chapter that follows the descriptive part.

Perhaps because the nominate family Doratodesmidae Cook, 1896 (cf. Cook 1896a) is very small, encompassing only 18 described valid species, and represents a rare group in Diplopoda, it benefits from rather complete historical reviews (Hoffman 1977a, 1982) and a key that is still relevant to all 13 nominate genera known to date (Zhang and Wang 1993). The following is a checklist of all hitherto named Doratodesmidae, arranged in alphabetical order.

(1) *Ascetophacus macclurei* Hoffman, 1977, the type species of *Ascetophacus* Hoffman, 1977, described and still known only from Batu Caves near Kuala Lumpur, Selangore State, Malaysia (Hoffman 1977a).

(2) *Ascetophacus reclinatus* Hoffman, 1977, described and still known only from two females taken from Cave Gua Anak Takun at Templer Park near Kuala Lumpur, Selangore State, Malaysia (Hoffman 1977b).

(3) *Cerastelachys cavernicola* (Sinclair, 1901), described as *Doratonotus cavernicola* Sinclair, 1901 from Cave Gua Tanan, Raman District and Cave Gua Glap near Biserat, Patani River, Patani District, southern Thailand; transferred to *Ascetophacus* by Hoffman (1977a), but later redescribed from type material and made the type species of *Cerastelachys* (Hoffman 1977b).

(4) *Crenatidorsus grandifoliatus* Zhang *in* Zhang & Wang, 1993, the type species of *Crenatidorsus* Zhang *in* Zhang & Wang, 1993, described from Daxiao Cave in Mile County and from Longbaopo Cave in Mengzi County, Yunnan (Wang and Zhang 1993), later also recorded from Chi Be Yi Cave

in Mengzi County, Yunnan, China (Golovatch 2003). Listed in Wang and Mauriès (1996).

(5) *Dimorphodesmus peculiaris* Murakami, 1966, the type species of *Dimorphodesmus* Murakami, 1966, described and still only known from two localities in Ehimé Prefecture, Shikoku, Japan (Murakami 1966).

(6) *Doratodesmus armatus* (Pocock, 1894), the type species of *Doratodesmus* Cook *in* Cook & Collins, 1895, a replacement name for the preoccupied *Doratonotus* Pocock, 1894 (Cook *in* Cook & Collins 1895). This species, which has been redescribed and illustrated from type material (Jeekel 1955), is now known from several localities in western Java, Indonesia (Pocock 1894). The redescriptions by Attems (1930, 1940) from female material collected in southern Sumatra, Indonesia actually concerned another species (Jeekel 1955). This apparently led Chamberlin (1945) to mistakenly redescribe the true *D. armatus* as a different genus and species, *Hoplitesmus enoplus* Chamberlin, 1945; both these names were synonymized by Jeekel (1955).

(7) *Doratodesmus beccarii* (Silvestri, 1895), originally described very succinctly and without illustrations in *Doratonotus* Pocock, 1894, a preoccupied name (Cook *in* Cook & Collins 1895); still known only from Mt Singalang, north-central Sumatra, Indonesia (Silvestri 1895).

(8) *Doratodesmus muralis* Cook, 1896, described from western Java, Indonesia (Cook 1896b), too succinctly to be recognizable (Jeekel 1955).

(9) *Doratodesmus vestitus* Cook, 1896, described from western Java, Indonesia (Cook 1896b), too succinctly to be recognizable (Jeekel 1955).

(10) *Dyomerothrix gremialis* Hoffman, 1982, the type species of *Dyomerothrix* Hoffman, 1982, described and still known only from "Chiang Dao caves" in northern Thailand (Hoffman 1982a). Listed in Enghoff (2005).

(11) *Eucondylodesmus elegans* Miyosi, 1956, the type species of *Eucondylodesmus* Miyosi, 1956, described and still known only from Izu Islands and several localities in Kanagawa Prefecture, Shikoku, Japan (Miyosi 1956).

(12) *Eutrichodesmus demangei* Silvestri, 1910, the type species of *Eutrichodesmus* Silvestri, 1910, described and still known only from Phu-Ly, Hanam Province, North Vietnam (Silvestri 1910). Listed in Enghoff et al. (2004).

(13) *Eutrichodesmus arcicollaris* Zhang *in* Zhang & Wang, 1993, described and still known only from Huayu Cave, Hekou County, Yunnan, China (Zhang and Wang 1993). Listed in Wang and Mauriès (1996).

(14) *Parapauroplus monodentus* Zhang *in* Zhang & Wang, 1993, the type species of *Parapauroplus* Zhang, in Zhang & Wang, 1993, described and still known only from Caiyun Cave, Mengla County, Yunnan, China (Zhang and Wang 1993). Listed in Wang and Mauriès (1996).

(15) *Pauroplus analdes* Chamberlin, 1945, the type species of *Pauroplus* Chamberlin, 1945, described and still known only from Lampongs, Pedada Bay, southwestern Sumatra, Indonesia (Chamberlin 1945).

(16) *Pocillidorsus dorsiangulatus* Zhang *in* Zhang & Wang, 1993, the type species of *Pocillidorsus* Zhang, in Zhang & Wang, 1993, described and still known only from Baoniujiao Cave, Mengla County, Yunnan, China (Zhang and Wang 1993). Listed in Wang and Mauriès (1996).

(17) *Scolopopyge pholeter* Hoffman, 1978, the type species of *Scolopopyge* Hoffman, 1978, described and still known only from Batip Cave, Finim Tel Plateau, Western Province, Papua-New Guinea (Hoffman 1977-78).

(18) *Selminarchus hispidus* Hoffman, 1978, the type species of *Selminarchus* Hoffman, 1978, described and still known only from Selminum Tem Cave, Finim Tel Plateau, Western Province, Papua-New Guinea (Hoffman 1977-78).

As one can easily see from the above list, most of the genera are monotypic and speciose genera are entirely absent. The distinguishing somatic features of Haplodesmidae and Doratodesmidae are so overwhelmingly abundant that they often provide enough information to describe/recognize species based on female material alone – a situation strongly reminiscent of that observed in the predominantly tropical family Pyrgodesmidae, which is one of the largest in Diplopoda. Like Haplodesmidae and Doratodesmidae, pyrgodesmids are usually small (<10 mm long), very heavily ornamented (hence showing numerous, distinct peripheral characters) and cryptic polydesmideans, especially common in forest litter, rotting wood and topsoil, only rarely occurring in caves. Unlike Haplodesmidae and Doratodesmidae, Pyrgodesmidae count over 170 genera (dozens of which are known from female or juvenile material only), the bulk of which are monotypic (Golovatch 1996). This alone is sufficient evidence of the poor state of the art concerning the taxonomy of these families.

Any group in which the species only slightly outnumber the genera can be viewed as a consequence of our highly imperfect knowledge of the group's real diversity, with numerous new species being anticipated to fill-in gaps between monotypic genera and to support abundant synonymies. Alternatively, the small number of species relative to genera may indicate that the group as a whole is relictual, and that most of the species in individual genera have become extinct. Our inclination is to consider this situation as being rooted in a combination of these factors: the still very fragmentary information currently available as regards the diversity of these families, even though one of them (Pyrgodesmidae) is amongst the largest in Diplopoda, and, above all, the wrong initial premises chosen for their classification. It is the emphasis placed on the numerous, often conspicuous peripheral characters, at the expense of the evolutionarily much more important and stable (but eventually more difficult to see and evaluate) gonopod traits, that has created the presently chaotic system of Pyrgodesmidae (e.g. Hoffman 1980; Golovatch 1996). To improve the situation and develop a reasonably balanced classification of Haplodesmidae s.l., we consider it necessary to rely chiefly on male genitalic characters (Hoffman 1977a, 1982a). In other words, it is the gonopod conformation, not the various details of somatic structure, however striking, that must be consistently applied to the elaboration of a revised generic-level classification. The present paper is the first step in this direction.

Abbreviations used

IZAS: Institute of Zoology, Academia Sinica, Beijing (China)
MCSNV: Museo Civico di Storia naturale, Verona (Italy)
MNHN: Muséum national d'Histoire naturelle, Paris (France)
NMNHS: National Museum of Natural History, Sofia (Bulgaria)
OBBFUL: Oddelek za biologijo, Biotehniska fakulteta, Univerza v Ljubljani (Biology Department, Biotechnical Faculty, University of Ljubljana), Ljubljana (Slovenia)
SCAU: South China Agricultural University, Guangzhou (China)
ZMUC: Zoological Museum, University of Copenhagen, Copenhagen (Denmark)
ZMUM: Zoological Museum, State University of Moscow, Moscow (Russia)
SEM: Scanning electron microscopy

Material and methods

The material serving as the basis for the present contribution derives from the predominantly subterranean collections made in Vietnam, China and Vanuatu by Anne Bedos and Louis Deharveng (MNHN), as well as by Boris Sket and his collaborators (OBBFUL) in Vietnam and China, by Petar Beron (NMNHS), Franck Bréhier (Moulis, France) and Leonardo Latella and his collaborators (MCSNV) in China, and by Josianne Lips (Villeurbanne, France) in Vanuatu. The bulk of this material, including most of the holotypes, has been deposited in MNHN, with two holotypes and several paratypes from China shared between the collections of SCAU and IZAS, and some further paratypes or non-types between the collections of NMNHS, MCSNV, ZMUC, ZMUM and OBBFUL, as indicated hereafter.

SEM micrographs were taken using a JEOL JSM-6480LV scanning electron microscope. After examination, SEM material was removed from stubs and returned to alcohol, all such samples being kept at MNHN.

Systematics

***Eutrichodesmus basalis* Golovatch, Geoffroy, Mauriès & VandenSpiegel, sp. n.**
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Figs 1-4.

Type material. Vietnam, Vinh Ha Long Prov. (SW), Dao Bo Hon, Hang Bo Nau Cave, 12.VI.2003, leg. P. Trontelj & B. Sket, holotype ♂ (MNHN JC 309), paratypes: 1 ♂ (MNHN JC 309), 1 ♀ (SEM).

Name. To emphasize the obvious basal position amongst the volvatory "doratodesmids".

Diagnosis. Differs from congeners by the apparently imperfect volvation, due to particularly short paraterga, coupled with an especially simple gonopod structure.

Description: Length of adults of both sexes *ca* 4.8-5.0 mm, width 0.6-0.65 mm, body broadest at segment 3 or 4; ♂♂ a little smaller than ♀♀. Holotype *ca* 4.8 mm long and 0.6 mm wide. Coloration uniformly pallid or light yellowish.

Adults with 20 segments, body subcylindrical (Fig. 1A), pattern of conglobation typical of "Doratodesmidae" as described by Golovatch (2003), but volvation itself obviously somewhat imperfect in barely concealing all (especially hind) legs (Figs 1A, C, D). Head (Fig. 2B) slightly transverse, rather densely pilose, microgranular amd microvillose just below antennae and on vertex, with a pair of paramedian,

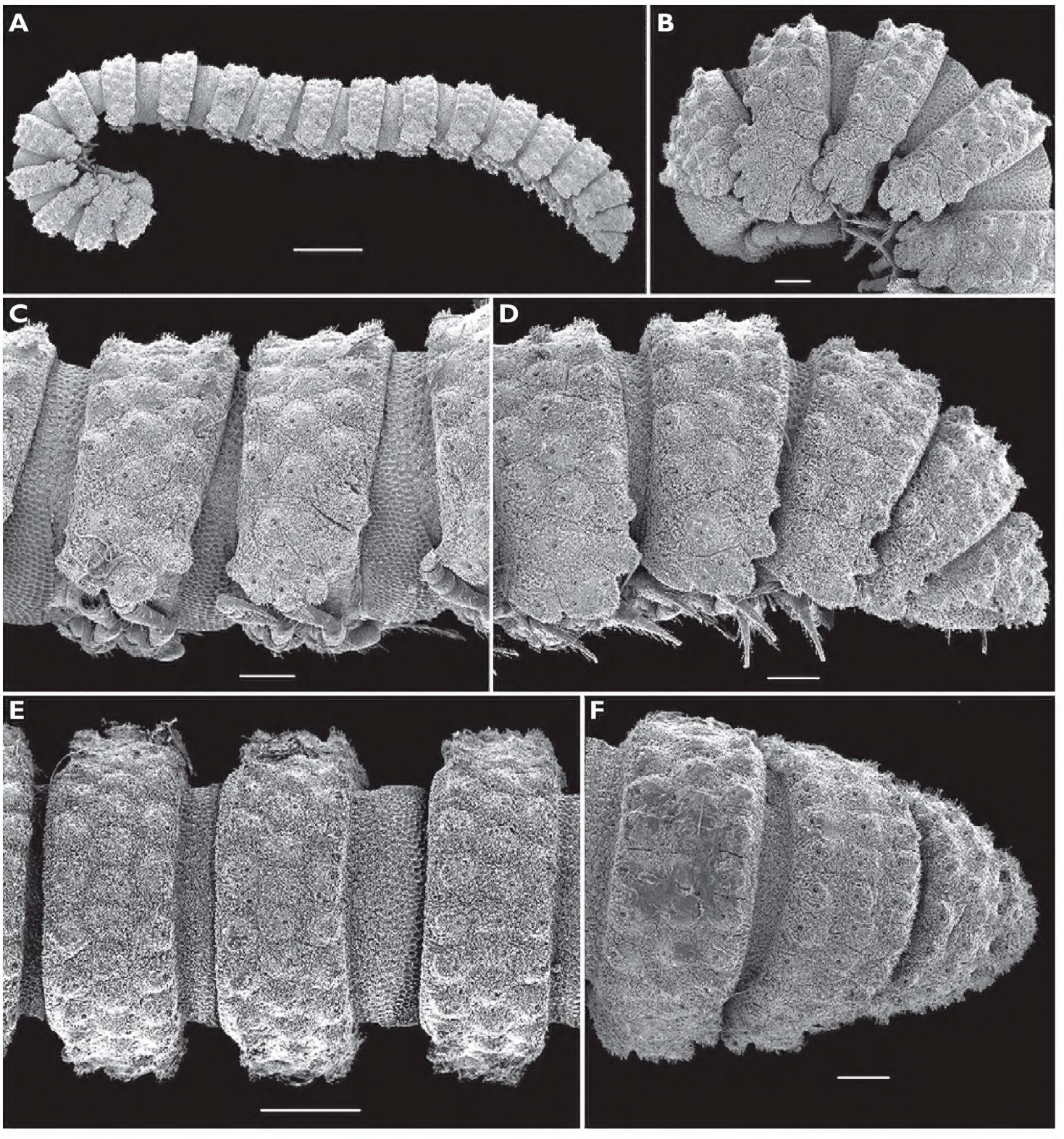

Figure 1. *Eutrichodesmus basalis* sp. n., ♀ paratype; **A**, habitus, lateral view; **B**, anterior part of body, lateral view; **C**, midbody segments, lateral view; **D**, posterior part of body, lateral view; **E**, midbody segments, dorsal view; **F**, posterior part of body, dorsal view. – Scale bars: A, 0.5 mm, B, C, D & F, 0.1 mm & E, 0.2 mm.

almost contiguous knobs; isthmus between antennal sockets very narrow. Antennae (Fig. 2C) very short and stout; antennomere 6 longer than 5, dorso-apically with an evident pit containing a tight group of minute bacilliform sensilla; antennomere 8 with the usual four sensory cones apically. Collum rather large, regularly convex, not covering the head from above, entire surface microvillose, with four transverse

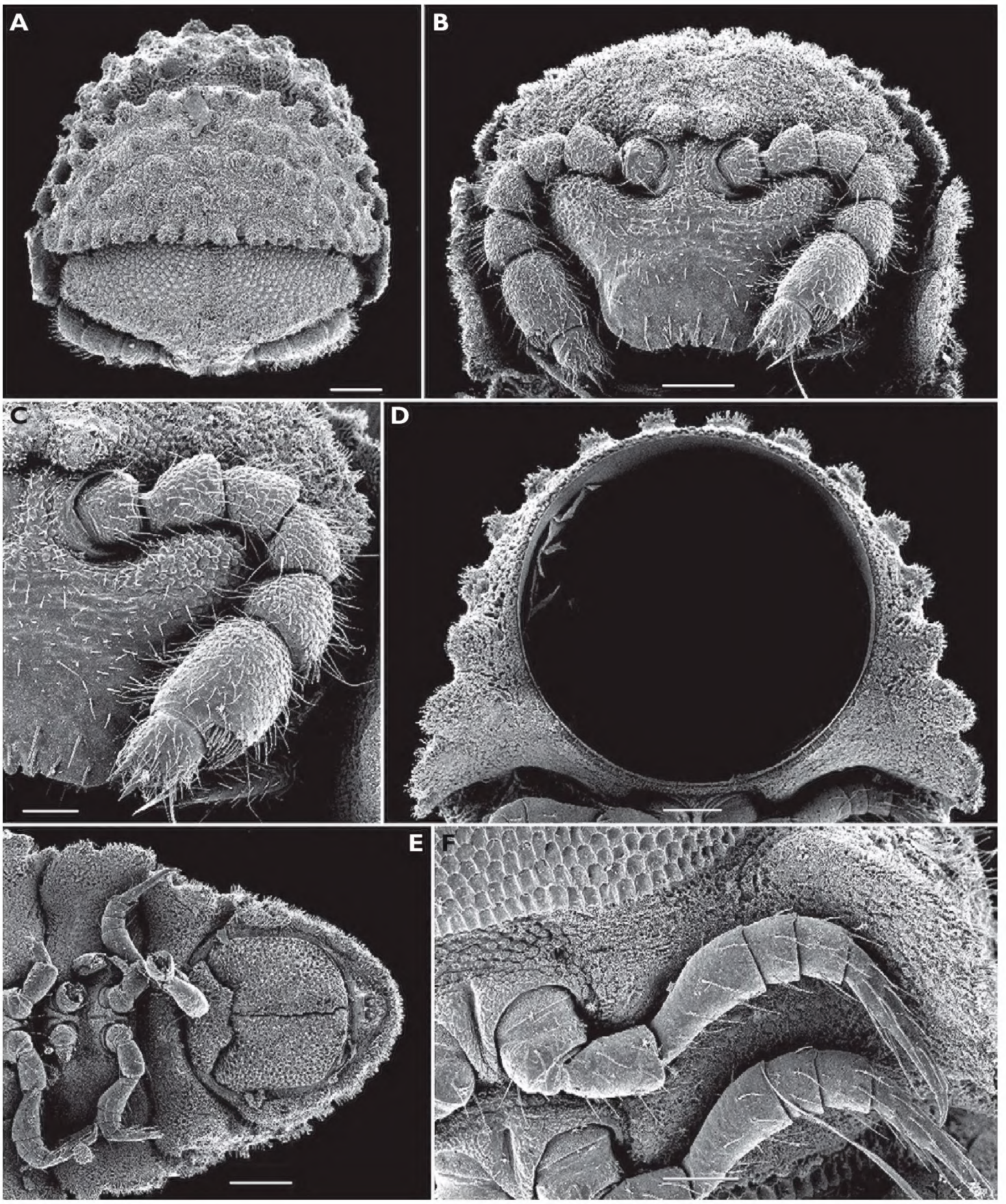

Figure 2. *Eutrichodesmus basalis* sp. n., ♀ paratype; **A**, anterior part of body, frontodorsal view; **B**, head, front view; **C**, antenna; **D**, cross-section of a midbody segment, caudal view; **E**, posterior part of body, ventral view; **F**, legs, ventral view. – Scale bars: A, B, D, E, 0.1 mm & C, F, 0.05 mm.

rows of round tubercles with a pit on top (apparently representing the former place of insertion of bisegmented, tactile setae, which are mostly lost) (Fig. 2A). Prozona very finely alveolate, collum and metaterga covered with a cerotegumental crust held by abundant microvilli; stricture between pro- and metazona broad and shallow, more finely alveolate-microgranular than prozona; limbus microcrenulate, nearly fully hidden by nearby abundant microvilli (Figs 3C, D). Metaterga behind collum with three transverse rows of tubercles (Figs 1A-F), some of which still retain long, bisegmented setae (Fig. 3B). Paraterga subvertical, very narrow, downwards barely reaching level of venter, clearly trisinuate caudolaterally at base due to two lobulations (Figs 1C, D; 2D; 3A); paraterga 2 strongly enlarged, with a series of lobulations anterolaterally, both schism and hyposchism very small; paraterga 3 and 4 slightly shorter than others (Fig. 1B), overlap of following paraterga typical, latter broadly rounded and evidently trilobate. Pore formula normal, ozopores located on top of a small porostele-like tubercle on ventrocaudal lobulation (Fig. 3A). Pleurotergal ridges very small, alveolate-microgranular like entire ventral surface. Epiproct short, also with tubercles, directed ventrocaudad, with the usual four cones (= spinneret setae) just below tip; para- and hypoprocts as in Figs 1F; 2E.

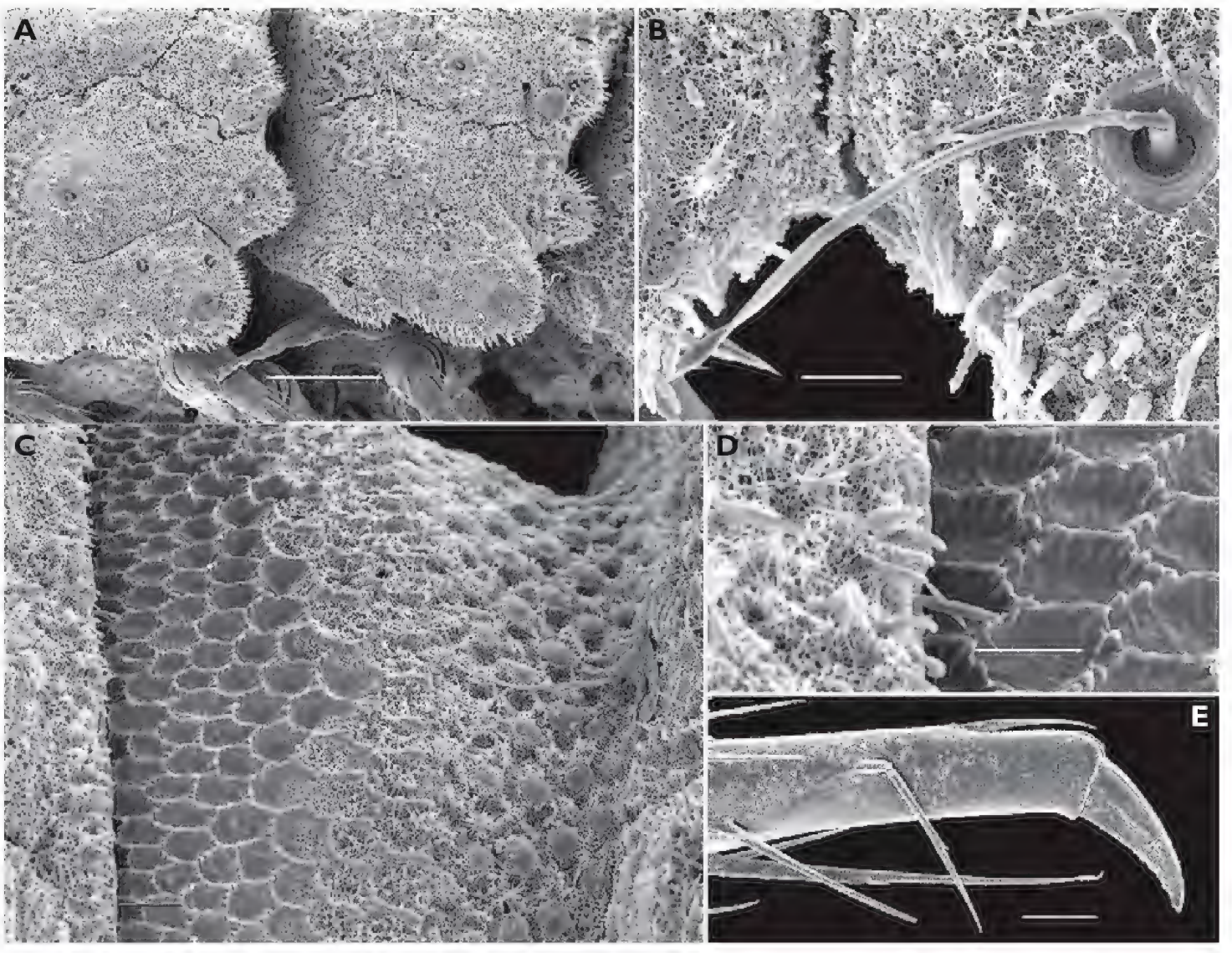

Figure 3. *Eutrichodesmus basalis* sp. n., ♀ paratype; **A**, enlarged paraterga with ozopores, lateral view; **B**, bisegmented seta; **C**, tegument texture; **D**, limbus and adjacent parts; **E**, claw. – Scale bars: A, 0.05 mm, B, D, E, 0.01 mm, C, 0.02 mm.

Sterna usually with a deep, narrow, longitudinal depression between coxae (Fig. 2F), but sterna between coxae 6, 7 and 9 much wider (Fig. 4A). Gonopod aperture transverse-oval, relatively small, far from reaching lateral sides of segment 7. Legs very short; tarsal segment longest; claw usual, simple, very slightly curved ventrad; some setae sparsely microdenticulate (Figs 2F; 3E).

Gonopods (Figs 4B, C) very simple. Coxae subquadrate, large, microtuberculate and abundantly setose ventrolaterally, with a conspicuous triangular lobe frontolaterally. Telopodite much longer than coxite, slender throughout, setose in its basal half, with a conspicuous, only apically denticulate, lateral, distofemoral process (dp) at about midway, with a hairpad in distal third, but seminal groove unexpectedly terminating subapically.

Remarks. This remarkable species somewhat bridges the former Haplodesmidae and Doratodesmidae. Hence the quotation marks which are used for "haplodesmids" and "doratodesmids" above and hereafter. In addition to showing the tergal trichome of peculiar, bisegmented setae and the unusually simple gonopods so characteristic of *Cylindrodesmus* (both features partly shared also with several true "doratodesmids"), it also, most importantly, has the body only capable of incomplete volvation, due to the relatively very short paraterga. Moreover, the ozopores are borne on small porostele-like

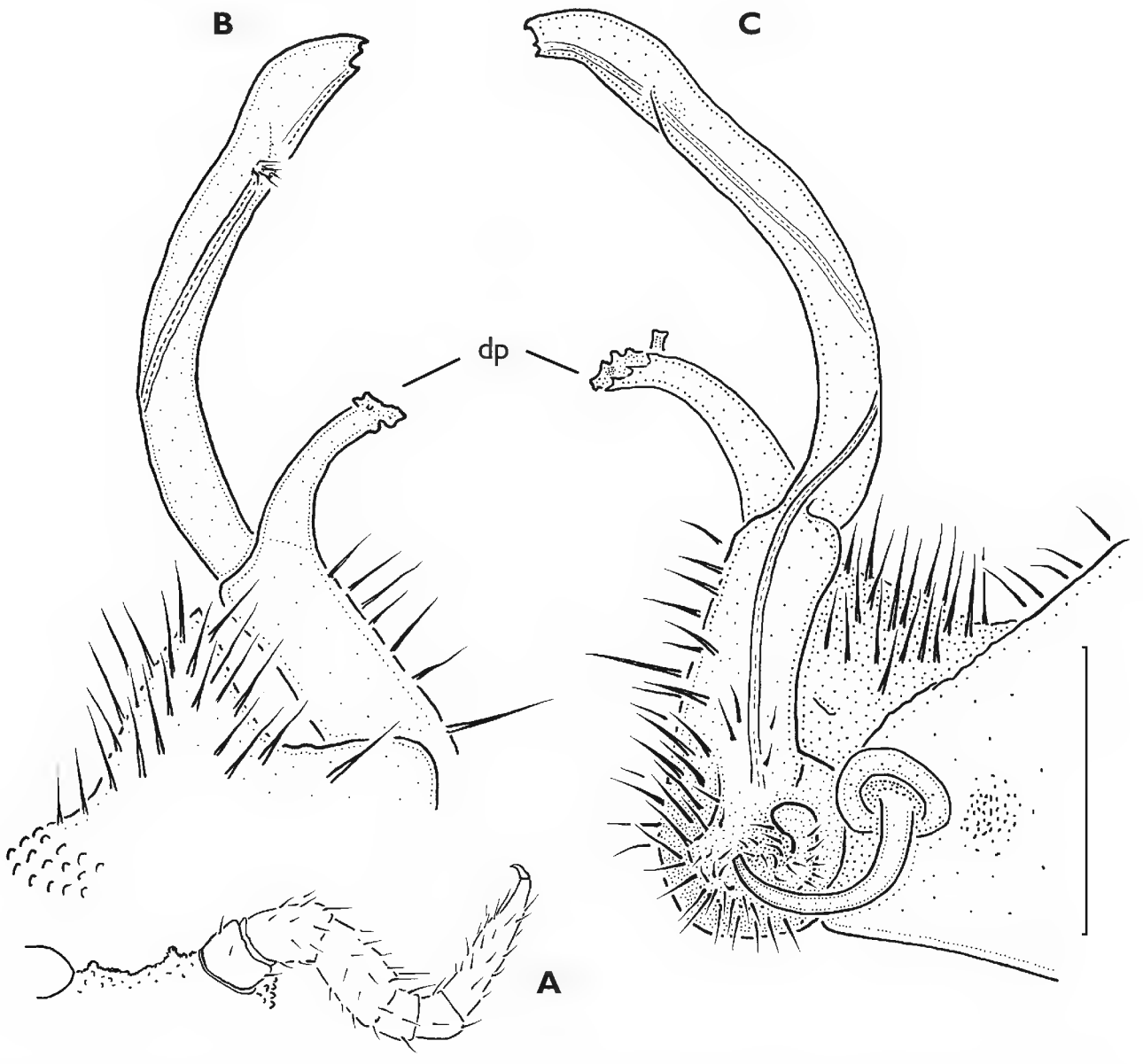

Figure 4. *Eutrichodesmus basalis* sp. n., ♂ paratype; **A**, leg 9, caudal view; **B & C**, left gonopod, mesal and lateral views, respectively (dp = distofemoral process). – Scale bar: A, 0.2 mm, B, C, 0.1 mm.

tubercles, a feature characteristic of most "haplodesmids", but only rarely encountered among "doratodesmids". At least the incomplete volvation and the simple biramous gonopods seem to be relatively primitive characters amongst the more advanced "doratodesmids" in which volvation is already perfect.

The new species especially resembles the similarly tuberculate-setose *Dyomerothrix gremialis* Hoffman, 1982 or *Parapauroplus monodentus* Zhang *in* Zhang & Wang, 1993, which also show rather simple gonopods (Hoffman 1982a; Zhang and Wang 1993).

***Eutrichodesmus armatocaudatus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, sp. n.**
urn:lsid:zoobank.org:act:B2718568-A85A-4FDE-80E9-574F67AB90E9
Figs 5-8.

Type material. Vietnam, Thanh Hoa Prov., Pu Luong, Lung Cao, Hang Lang Lua Cave, 11.XII.2003, leg. L. Deharveng & team (Vn0312-05), holotype ♂ (MNHN JC 310), paratypes: 1 ♂, 1 juv. (MNHN JC 310), 1 ♂ (ZMUM); Ha Nam Ninh Prov., Cuc Phuong National Park, Cave of Prehistoric Man, 10.X.1998, leg. L. Deharveng (VIET-537), 1 ♂ (MNHN JC 310); same locality, Water Fairy Cave, 11.X.1998, leg. L. Deharveng (VIET-541), 1 ♂, 2 juv. (MNHN JC 310); same locality, cave 4 (Son Cung Cave?), 21.VI.2003, leg. P. Trontelj & B. Sket, 1 ♂, 1 ♀, 3 juv. (MNHN JC 310), 1 ♂, 1 juv. (ZMUC), 1 ♂, 1 juv. (NMNHS), 1 ♂ (MCSNV), 1 ♂, 1 juv. (OBB-FUL), 1 ♀ (SEM); Ha Nam Ninh Prov., outside Cuc Phuong National Park, cave 3, 20.VI.2003, leg. P. Trontelj & B. Sket, 1 ♂, 1 ♀ (ZMUM).

Name. To emphasize the obvious dorsal projections on body segments 17-19.

Diagnosis. Most similar to *Parapauroplus monodentus* Zhang *in* Zhang & Wang, 1993, which also shows evident mid-dorsal projections only on body segments (16)17-19, but differs by the presence of porosteles, the slightly lower metatergal tubercles devoid of microsetae near each of the main setae, and the slightly stouter gonopod telopodite showing a shorter midway process.

Description. Length of adults of both sexes *ca* 10-14 mm, width 2.3-2.6 mm, body broadest at segment 3 or 4; ♂♂ usually a little smaller than ♀♀. Holotype *ca* 11 mm long and 2.5 mm wide. Coloration uniformly pallid or light yellowish.

Adults with 20 segments, pattern of conglobation typical of "Doratodesmidae" (Figs 5A). Head (Fig. 6A) and tegument (Figs 5B, C; 6F, G) as in preceding species, but antennae somewhat longer (Fig. 6A), collum slightly flattened mid-dorsally, not covering the head from above (Fig. 6A). Metaterga behind collum with three transverse, rather irregular rows of tubercles (Figs 5A-C), most of which still retain short, bisegmented setae (Fig. 6G), metaterga 17-19 each with an evident dorsal outgrowth (Fig. 5C). Paraterga mostly directed ventrolaterad, rather broad, slightly surpassing level of venter, clearly trisinuate caudolaterally at base, due to two lobulations (Figs 5B, D; 6B); paraterga 2 strongly enlarged, subvertical, margin nearly entire, with only very faint traces of a series of small lobulations anterolaterally (Fig. 6A), both schism and hyposchism very small; paraterga 3 and 4 slightly shorter than others, overlap of

following paraterga typical, latter broadly rounded and slightly 3- or 4-lobate. Limbus spiculate (Fig. 6F). Pore formula normal, ozopores located on top of a small porostele, slightly above ventrocaudal lobulation (Figs 6C-E). Pleurotergal carinae wanting. Epiproct elongated, also with tubercles, directed ventrocaudad, with the usual four cones just below tip; para- and hypoprocts as in Figs 5E, F.

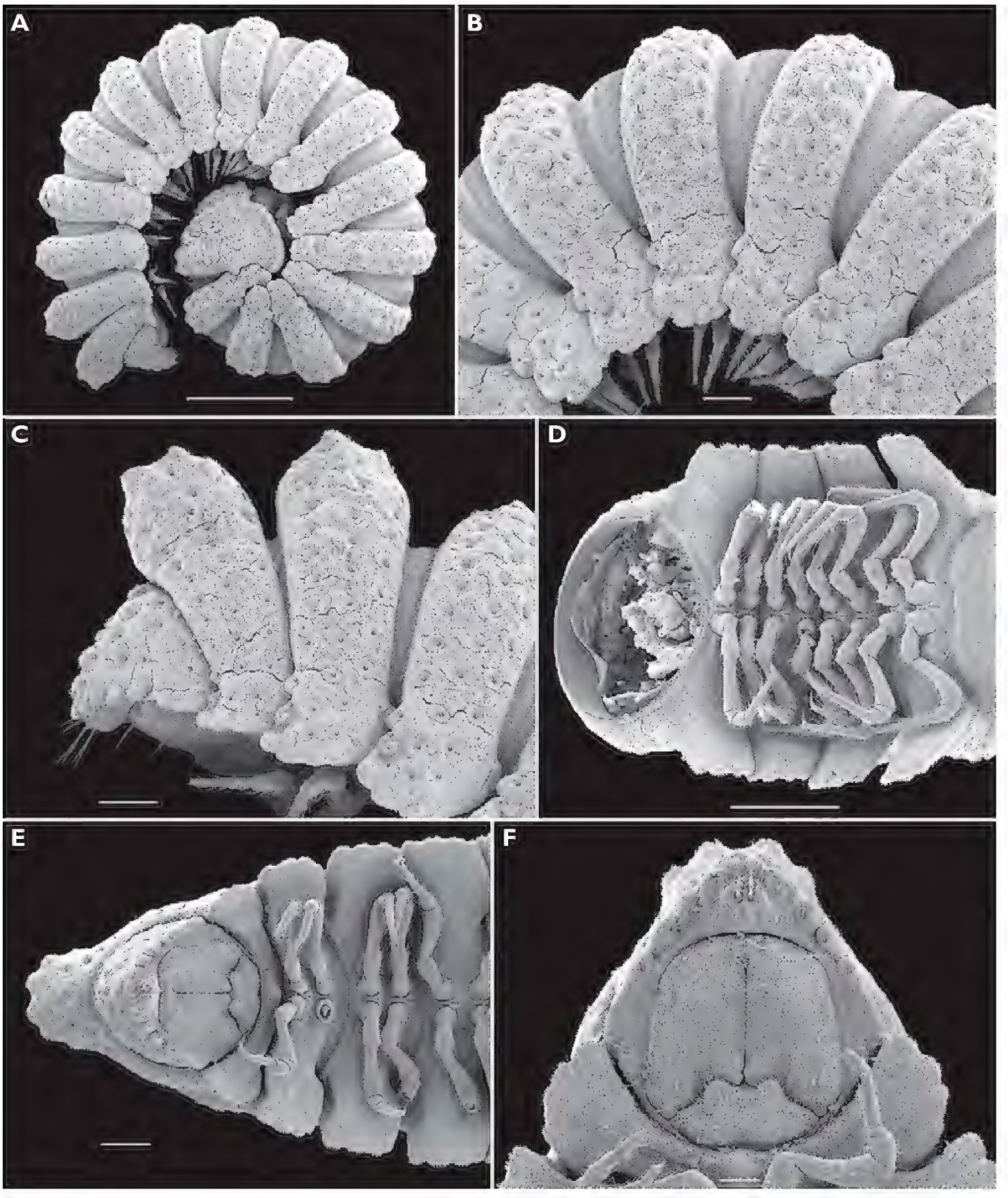

Figure 5. *Eutrichodesmus armatocaudatus* sp. n., ♂ paratype from cave 4; **A**, habitus, lateral view; **B**, midbody segments, lateral view; **C**, posterior part of body, lateral view; **D**, midbody segments, ventral view; **E**, posterior part of body, ventral view; **F**, telson, ventral view. – Scale bars: A, 1.0 mm, B, C, E, 0.2 mm, D, 0.5 mm & F, 0.1 mm.

Sterna usually with a deep, narrow depression between coxae (Figs 5D; 6B), only sterna between coxae 6, 7 and 9 much wider (Fig. 7A). Gonopod aperture transverse-oval, relatively small, far from reaching lateral sides of segment 7. Legs relatively long; femoral and tarsal segments longest and equal; claw simple, very slightly curved ventrad; some setae very sparsely microdenticulate (Figs 5D; 6B).

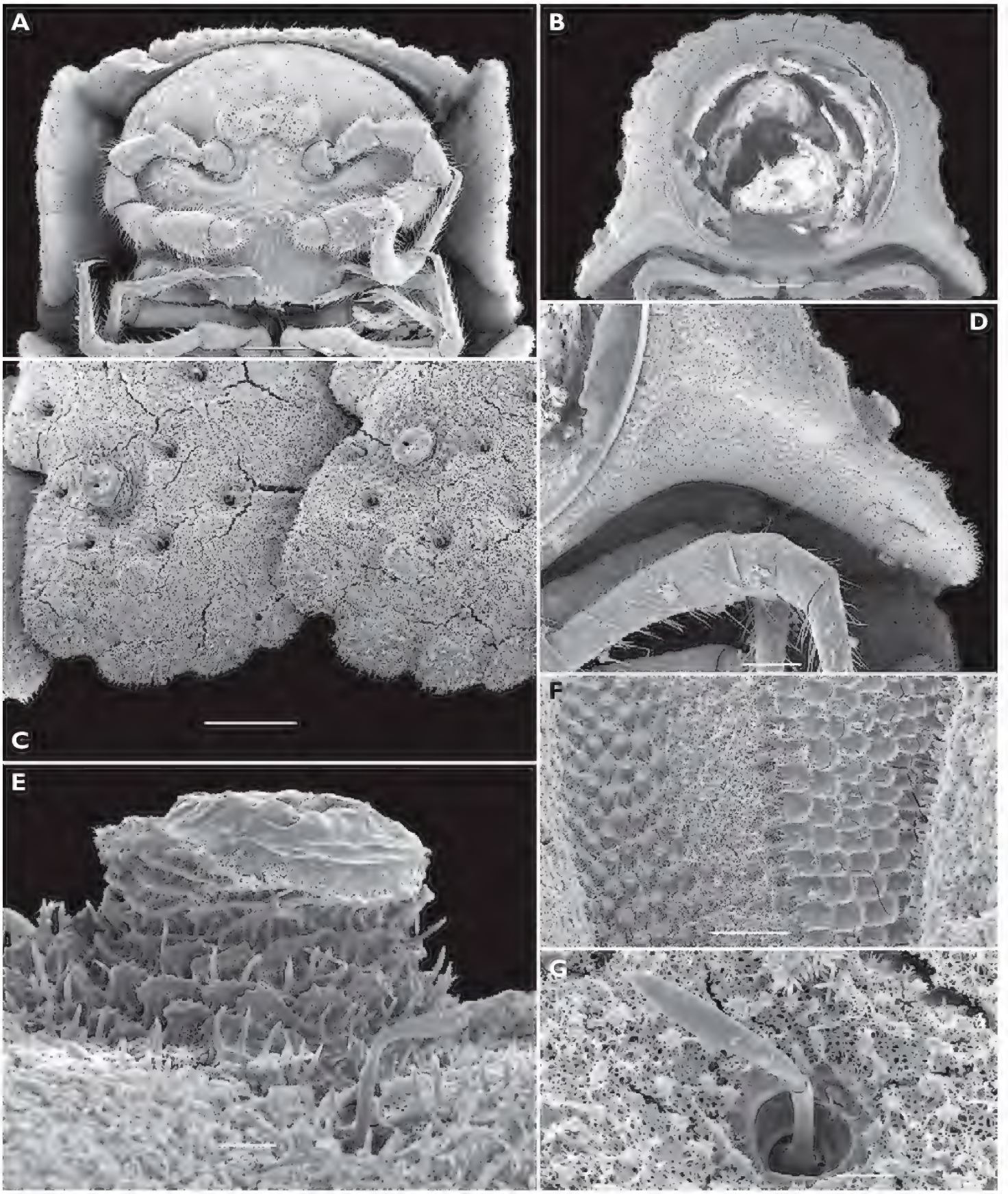

Figure 6. *Eutrichodesmus armatocaudatus* sp. n., ♂ paratype from cave 4; **A**, anterior part of body, frontoventral view; **B**, cross-section of a midbody segment, caudal view; **C**, enlarged paraterga with ozopores, lateral view; **D**, paratergum with porostele, caudal view; **E**, porostele; **F**, texture of prozonite and limbus; **G**, cerotegument with a bisegmented seta. – Scale bars: A, B, 0.2 mm, C, D, 0.1 mm, E, G, 0.01 mm & F, 0.05 mm.

Figure 7. *Eutrichodesmus armatocaudatus* sp. n., ♂ paratype from cave 4; **A**, body segments 6 and 7, ventral view; **B**, gonopods, ventral view; **C**, same, ventral view; **D**, gonopod apices. – Scale bars: A, 0.5 mm, B, 0.2 mm, C, 0.05 mm & D, 0.02 mm.

Gonopods (Figs 7; 8) very simple. Coxae subquadrate, large, microtuberculate and abundantly setose ventrolaterally, with a conspicuous rounded lobe frontolaterally. Telopodite considerably longer than coxite, slightly stouter, setose in its basal half, with an inconspicuous, digitiform, simple, lateral, distofemoral process (dp) at about midway, more distally with a slightly folded and enlarged shaft (= solenomere) with dense pilosity and a hairpad; seminal groove terminating subapically, acropodite short.

Remarks. This species seems to be close to some of the "doratodesmids" showing evident mid-dorsal projections on some of the metaterga, e.g. *Ascetophacus macclurei* Hoffman, 1977, *Cerastelachys cavernicola* (Sinclair, 1901), *Pocillidorsus dorsiangulatus* Zhang *in* Zhang & Wang, 1993 and *Parapauroplus monodentus* Zhang *in* Zhang & Wang, 1993, etc. (Hoffman 1977a, 1977b; Zhang and Wang 1993).

Cave 4 also supports another millipede, *Glyphiulus mediobliteratus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2007 (Golovatch et al. 2007b).

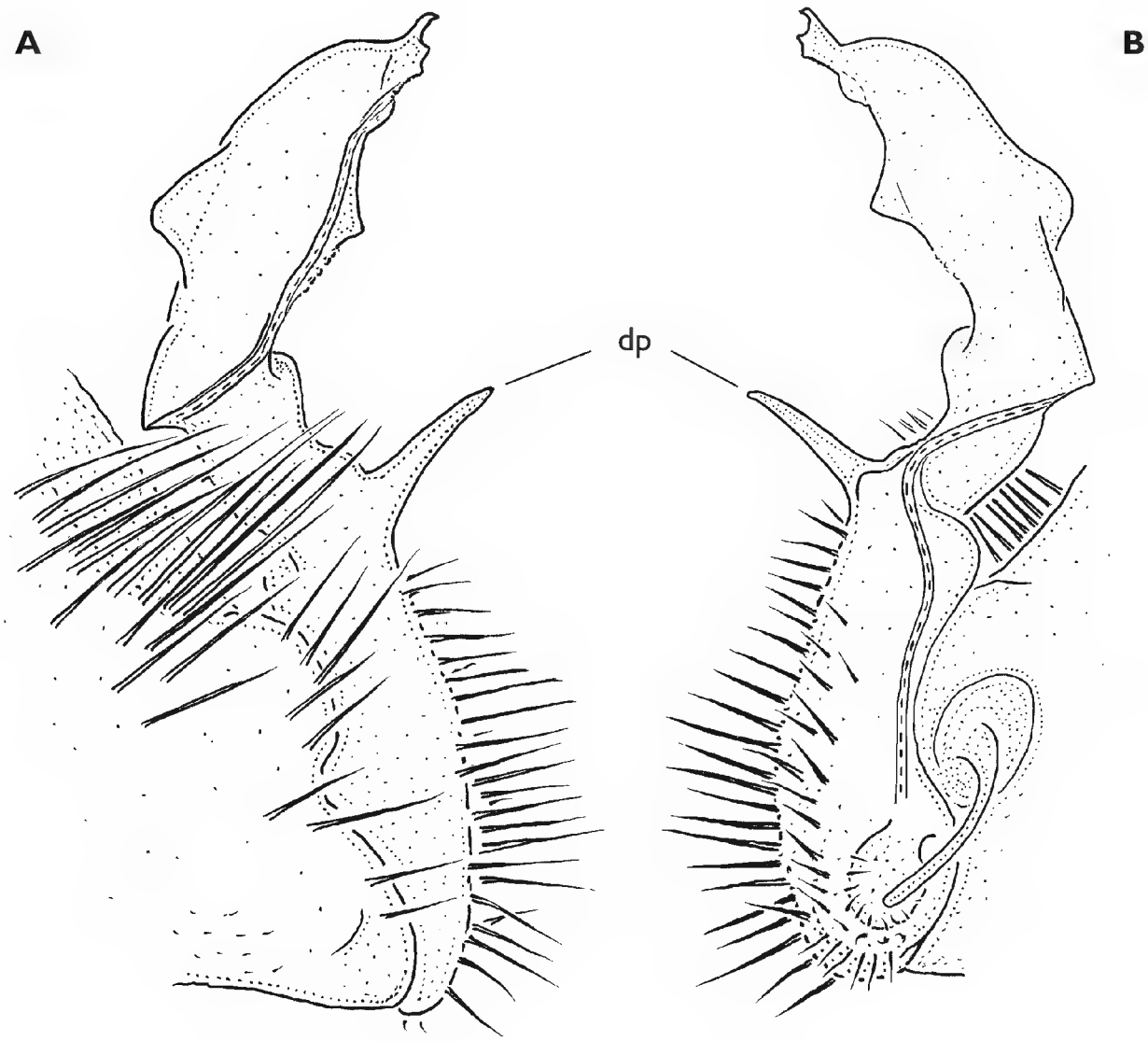

Figure 8. *Eutrichodesmus armatocaudatus* sp. n., ♂ paratype from cave 4; **A & B**, right gonopod, mesal and lateral views, respectively (micropilosity not shown; dp = distofemoral process). – Scale bar: 0.2 mm.

***Eutrichodesmus communicans* Golovatch, Geoffroy, Mauriès & VandenSpiegel, sp. n.**
urn:lsid:zoobank.org:act:8293BC13-BF5A-4E2F-BCEE-0711CFC4C86E
Figs 9-13.

Type material. Vanuatu, Espirito Santo, Malo Island, Avorani, forest litter, Berlese extraction, 15.IX.2006, leg. L. Deharveng & A. Bedos (SK06-15/06), holotype ♂ (MNHN JC 311), paratypes: 1 ♂, 4 ♀♀ (MNHN JC 311), 1 ♂, 1 ♀ (ZMUM), 1 ♀ (NMNHS), 1 ♀ (MCSNV), 1 ♀ (ZMUC); same place, date and collectors (SK06-15/13), 1 ♂, 1 ♀, 1 juv. (MNHN JC 311); Espirito Santo, Fapon doline 3, 5.IX.2006, leg. L. Deharveng & A. Bedos (SK06-15/18), 5 ♀♀, 4 juv. (MNHN JC 311), 1 ♂ (SEM); Espirito Santo, very humid forest at Boutmas Pass, 27.IX.2006, leg. L. Deharveng & A. Bedos (SK06-27/12), 1 ♂ (MNHN JC 311); Espirito Santo, Boutmas, forest above Jourdain River, Berlese extraction of litter, 27.IX.2006, leg. L. Deharveng & A. Bedos (SK06-27/09), 1 ♂ (MNHN JC 311); Espirito Santo, Boutmas, Fapon doline 2, 5.IX.2006, leg. L. Deharveng & A. Bedos (SK06-05/12), 2 ♀♀ (MNHN JC 311); Espirito Santo, Funatus, Katae Cave, Berlese extraction of guano, 18.09.2006, leg. J. Lips (SK06-18/07, Katae 4gu), 1 ♂, 2 juv. (ZMUC).

Figure 9. *Eutrichodesmus communicans* sp. n., ♂ paratype from Malo Island, habitus.

Name. To emphasize a superficial transition from a still non-volvatory "haplodesmid" condition to the typical, fully volvatory "doratodesmid" one.

Diagnosis. Differs from congeners by the tergal trichome being composed of only very long, bisegmented, tactile setae, coupled with the gonopod telopodite having a peculiar, dentate-microtuberculate, lateral process at midway and a lobiform, slightly coiled distal part.

Description. Length of adults of both sexes *ca* 3.5-4.2 mm, width 0.6-0.75 mm, body broadest at segment 3 or 4; ♂♂ usually a little smaller than ♀♀. Holotype *ca* 3.8 mm long and 0.65 mm wide. Coloration uniformly pallid, ranging from white to light yellow or pink.

Adults with 19 segments, body subcylindrical (Figs 9; 10A), pattern of conglobation typical of "Doratodesmidae", but volvation itself barely complete, poorly concealing at least legs of several caudal segments. Head (Figs 10E, F; 11A, B) slightly transverse, rather densely pilose, microgranular; isthmus between antennal sockets very narrow.

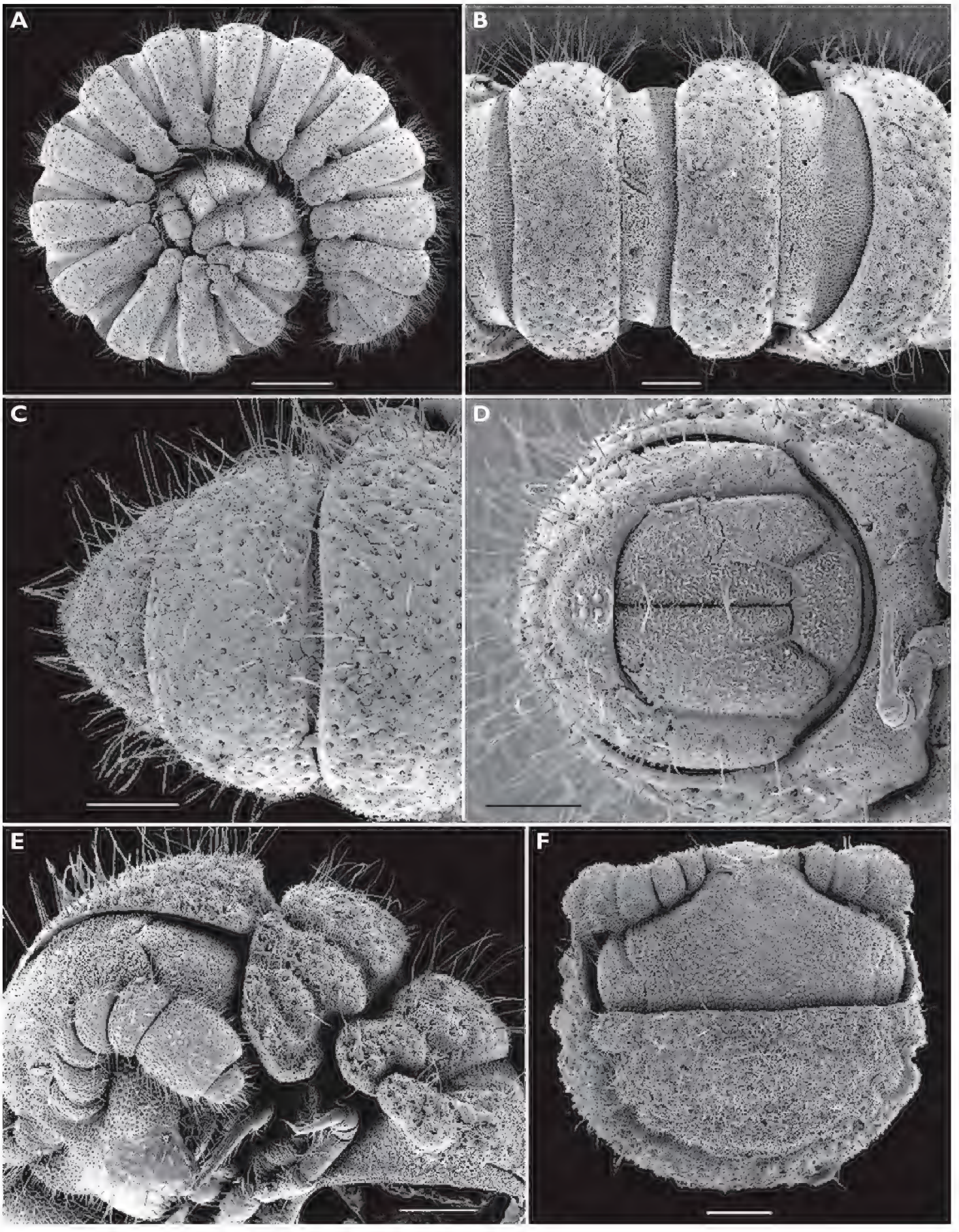

Figure 10. *Eutrichodesmus communicans* sp. n., ♂ paratype from Fapon doline 3; **A**, habitus, lateral view; **B**, midbody segments, dorsal view; **C**, posterior part of body, dorsal view; **D**, same, ventral view; **E**, anterior part of body, ventrolateral view; **F**, same, front view. – Scale bars: A, 0.2 mm, B-F, 0.1 mm.

Antennae (Figs 11C, D) very short and stout; antennomere 6 longer than 5, dorsoapically with an evident pit containing minute bacilliform sensilla; antennomere 8 with usual four sensory cones apically. Collum rather large, even and convex, not covering

the head from above, very densely and irregularly setose, setae bisegmented, tactile (Fig. 10F). Prozona very finely alveolate, collum and metaterga covered with a rather even cerotegumental crust held by microvilli, this crust, like on collum, being perforated only by dense, irregularly arranged, tactile, bisegmented setae; stricture between pro- and metazona broad and shallow, even more finely alveolate than prozona; limbus entire, not

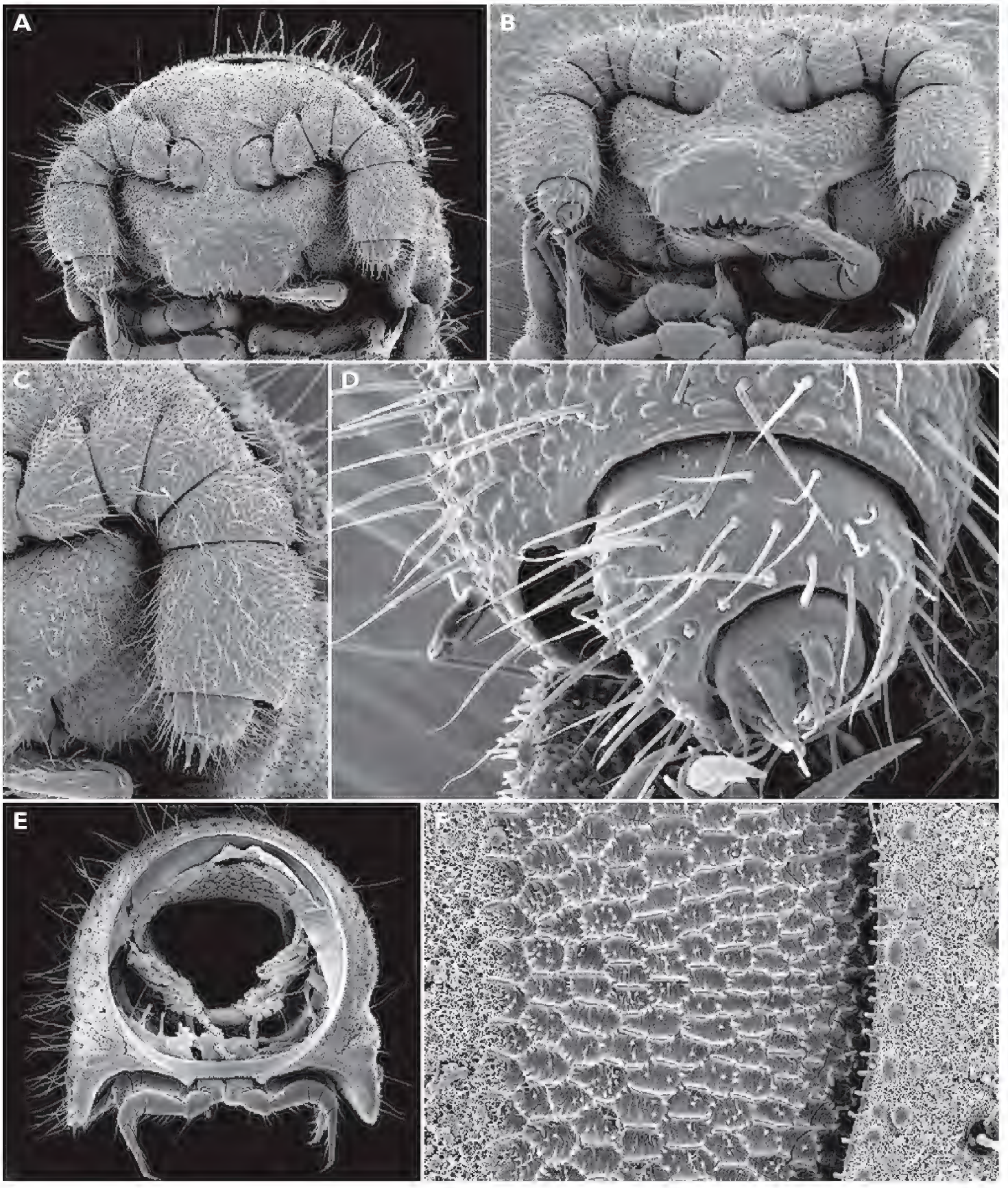

Figure 11. *Eutrichodesmus communicans* sp. n., ♂ paratype from Fapon doline 3; **A**, anterior part of body, ventral view; **B**, same, ventrocaudal view; **C**, antenna; **D**, apex of antenna; **E**, cross-section of a midbody segment, caudal view; **F**, texture of prozonite and limbus. – Scale bars: A, B, E, 0.1 mm, C, 0.05 mm, D, 0.01 mm & F, 0.02 mm.

hidden by sparse microvilli (Figs 11F; 12A-C). Paraterga subvertical and rather narrow, weakly set off by 1-2 shallow depressions or sulci, slightly bisinuate caudally at base (Figs 10E; 11E); paraterga 2 strongly enlarged, schism and hyposchism very small; paraterga

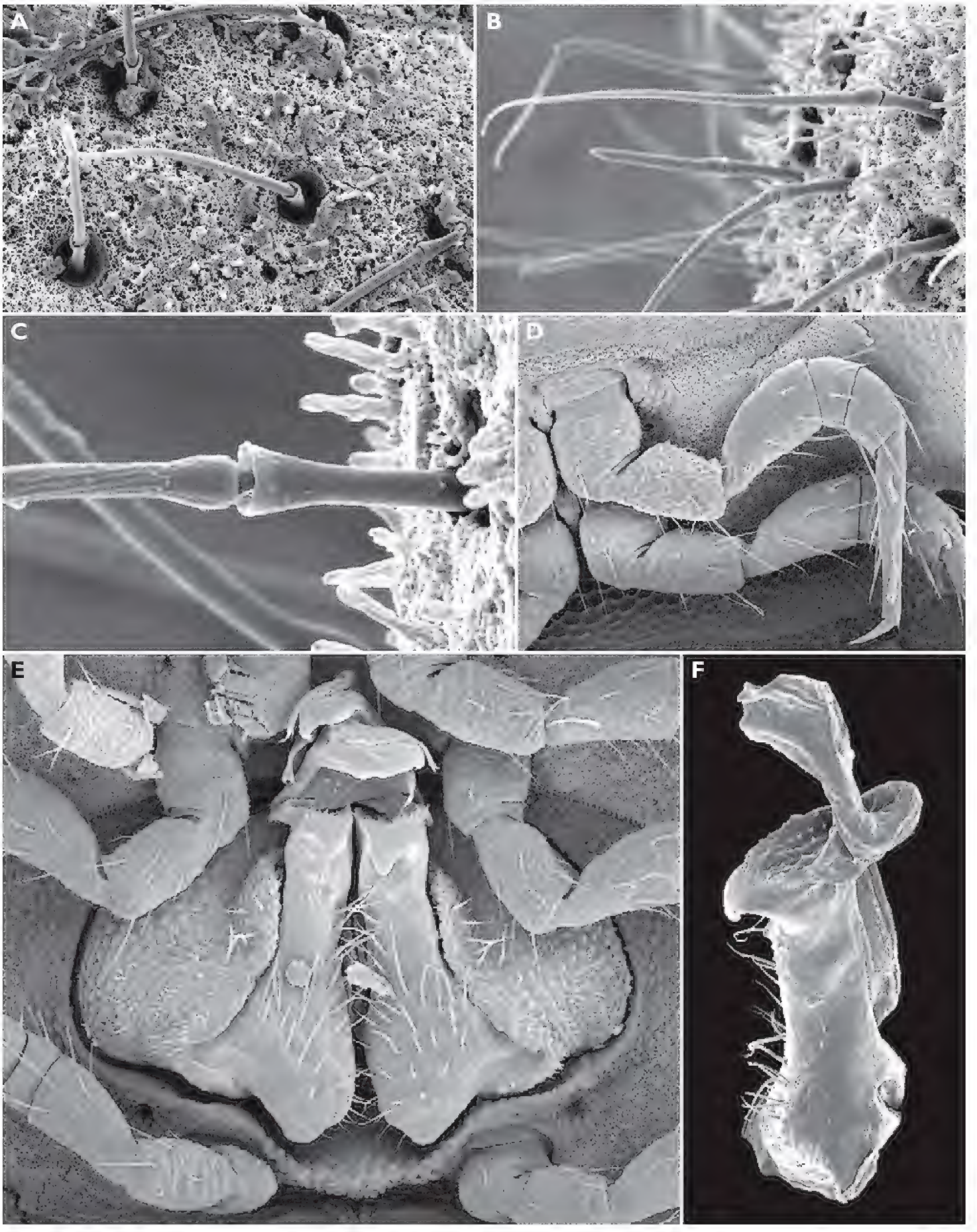

Figure 12. *Eutrichodesmus communicans* sp. n., ♂ paratype from Fapon doline 3; **A**, metatergal cerotegument and bisegmented setae; **B**, same with microvilli, lateral view; **C**, same with base of a bisegmented seta; **D**, legs, ventral view; **E**, gonopods, ventral view; **F**, left gonopod, dorsolateral view. – Scale bars: A, B, 0.01 mm, C, 0.005 mm, D, F, 0.05 mm.

3 and 4 shorter than others (Figs 9; 10A, E), following paraterga broadly rounded, overlap typical. Pore formula normal, ozopores located near ventral margin, progressively closer to caudal corner of paraterga. Pleurotergal ridges very small, microgranular like entire ventral surface (Fig. 11E). Epiproct short, slightly uneven, directed ventrocaudad, below tip with the usual four cones; para- and hypoproct as in Figs 10C, D.

Sterna usually with a minute middle knob separating bases of nearly contiguous coxae (Fig. 12D), only sterna between coxae 6, 7 and 9 much wider (Fig. 12E). Gono-

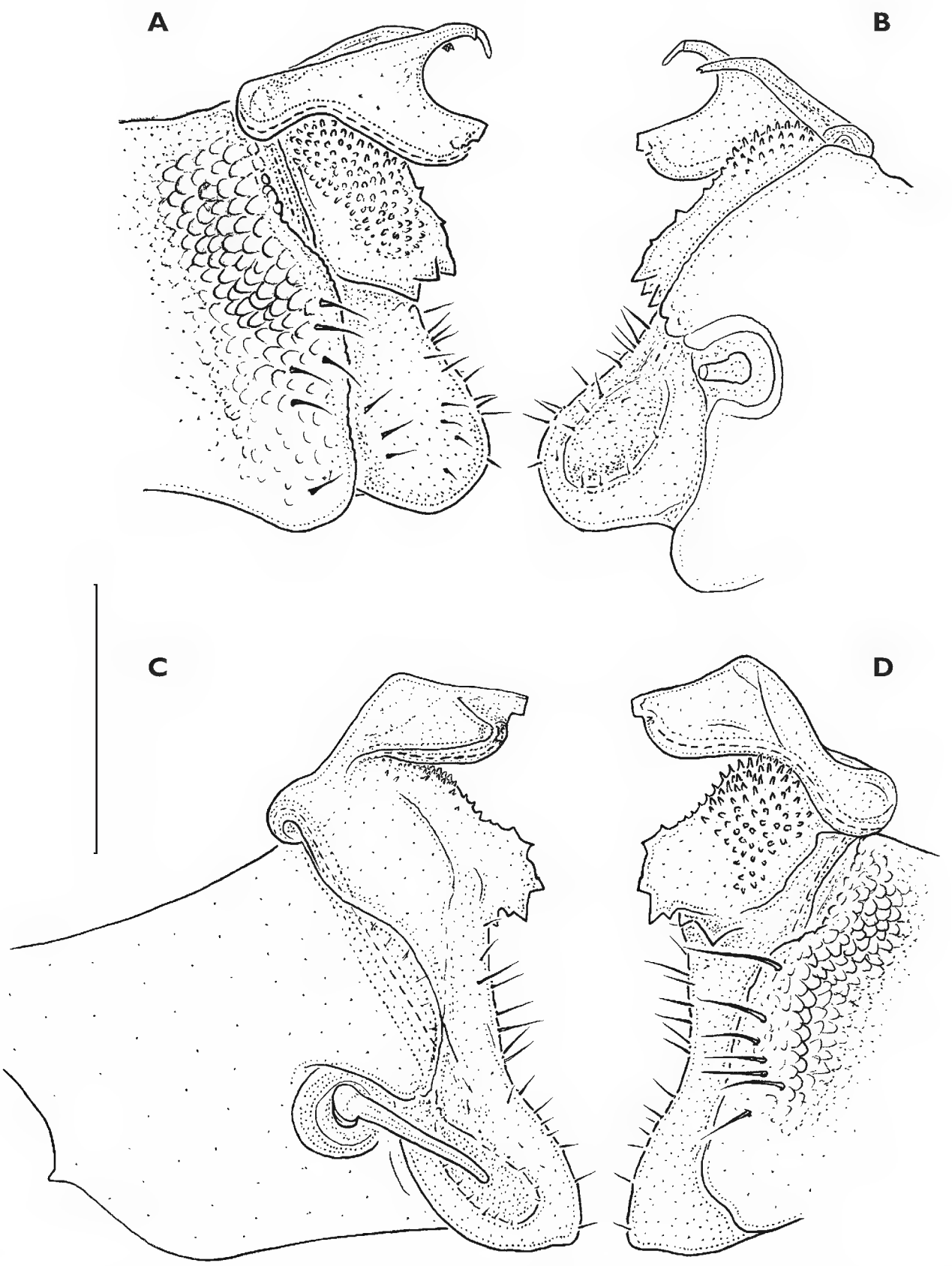

Figure 13. *Eutrichodesmus communicans* sp. n., ♂ paratype from Boutmas; **A-D**, left (A, B) and right (C, D) gonopods, lateral, mesal, mesal and lateral views, respectively (dp = distofemoral outgrowth). – Scale bar: 0.2 mm.

pod aperture transverse-oval, relatively small, far from reaching lateral sides of segment 7, as in Fig. 12E. Legs relatively short; coxae and prefemora microgranular; tarsal segment longest; claw usual, simple, very slightly curved ventrad; some setae very sparsely microdenticulate (Fig. 12D). Coxae 1 of ♂ with a distinct distomedial spine, coxae 2 of ♂ perforated by vas deferens (Fig. 11B).

Gonopods (Figs 12E, F; 13) rather complex. Coxae subquadrate, very large, scaly, with only a few setae ventrolaterally. Telopodite only slightly longer than coxite, its basal part setose and slender, with a conspicuous, densely dentate-tuberculate, distofemoral outgrowth (dp) at about midway, more distally with an expanded, somewhat folded, coiled, broadly trifid lobe, carrying a very short solenomere branchlet laterally.

Remarks. This remarkable species partly bridges the former Haplodesmidae and Doratodesmidae in showing the tergal trichome of peculiar, bisegmented setae so characteristic of *Cylindrodesmus* (in which, however, it is mixed with usual setation), also shared with several true "doratodesmids", on the one hand, and the body and gonopod structure of a rather typical "doratodesmid", on the other.

***Eutrichodesmus latus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, sp. n.**
urn:lsid:zoobank.org:act:FE7F4D6B-F489-4D30-900B-9A3E4F3D1BB9
Figs 14-17.

Type material. China, Guangxi Prov., Yachang Nature Reserve, Yan Wu Dong Cave, 31.05.2007, leg. L. Deharveng & A. Bedos (CHI-GX07-31/01), holotype ♂ (IZAS), paratypes: 2 ♂♂, 6 ♀♀ (MNHN JC 312), 1 ♂ (SEM); same locality, Xia Yan Dong Cave, 28.V.2007, leg. L. Deharveng & A. Bedos (CHI-GX07-28/01), 5 ♂♂ (SCAU); same locality, Xiao Shui Dong Cave, 2.VI.2007, leg. F. Bréhier (CHI-GX07-02/07), 4 ♀♀, 1 juv. (IZAS); same locality, She Dong Cave, 30.V.2007, leg. F. Bréhier (CHI-GX07-30/08), 2 ♂♂, 1 ♀, 1 juv. (SCAU), 1 ♂, 1 ♀, 1 juv. (ZMUM), 1 ♂ (ZMUC), 1 ♂ (NMNHS), 1 ♂ (MCSNV).

Name. To emphasize the broad paraterga.

Diagnosis. Differs from all congeners except *E. similis* sp. n. by the very broad and mostly only slightly declivous paraterga, such that volvation is apparently imperfect, from *E. similis* sp. n. by the collum bearing no row of peculiar teeth along its entire front margin, and the gonopods being less enlarged and simpler distally.

Description. Length of adults of both sexes *ca* 11-13 mm, width 2.4-3.0 mm, body broadest at segments 5-16. Holotype *ca* 12 mm long and 3.0 mm wide. Coloration uniformly yellow-brown to brownish, sometimes slightly marbled.

Adults with 20 segments (Fig. 14A), conglobation pattern typical of "Doratodesmidae", but volvation apparently imperfect because of paraterga being too broad and mostly only slightly declivous, leaving small lacunae laterally even when body maximally enrolled. Head (Figs 14F; 15A) and tegument (Figs 15E, F) basically as in preceding species, but antennae somewhat longer, antennomeres 3 and 6 of subequal length (Fig. 14F), collum not covering the head from above, slightly elevated

frontolaterally, with 4-5 irregular rows of mostly flat tubercles/bosses, including a row of more distinct cones at caudal edge (Figs 15A, B). Metaterga behind collum with three transverse, rather irregular rows of similarly flat tubercles, most of which still retain short, bisegmented setae (Fig. 15A, B, D-F); limbus microcrenulate. Paraterga with evident shoulders anteriorly, mostly directed laterad, only slightly declivous, very broad, tips about level with venter, very distinctly crenulate caudolaterally (Figs 14A-E; 15C, D); paraterga 2 rather strongly enlarged, directed ventrolaterad, lateral margin evidently quadrilobulate, both schism and hyposchism small; paraterga 3 and

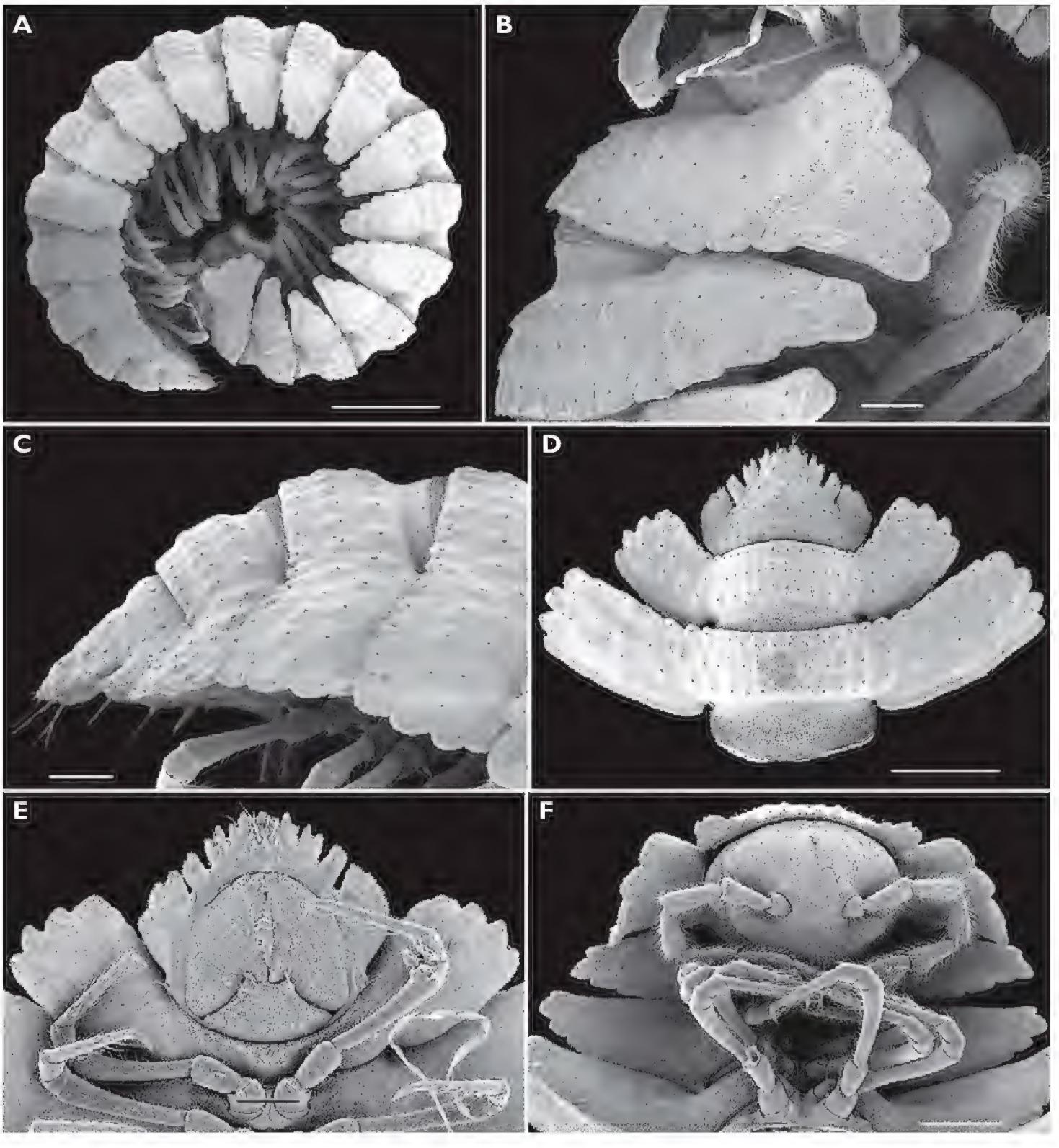

Figure 14. *Eutrichodesmus latus* sp. n., ♂ paratype from Yan Wu Dong Cave; **A**, habitus, lateral view; **B**, anterior part of body, lateral view; **C**, posterior part of body, lateral view; **D**, same, dorsal view; **E**, same, ventral view; **F**, anterior part of body, ventral view. – Scale bars: A, 1.0 mm, B, C, E, 0.2 mm, D, F, 0.5 mm.

4 slightly shorter than others, bilobate laterally (Figs 14B; 15B), following paraterga more broadly rounded and quadrilobulate, overlap typical. Pore formula normal, ozopores located at base of ventrocaudal lobulation (Fig. 15D). Pleurotergal carinae wanting. Epiproct strongly flattened, dorsally also tuberculate, with several deep incisions at lateral edge, directed ventrocaudad, with the usual four cones just below tip; para- and hypoprocts as in Figs 14C-E.

Sterna usually with a rather deep, narrow depression between coxae (Fig. 16A), only those between coxae 7 and 9 much wider (Fig. 16B). Gonopod aperture transverse-oval, relatively small, far from reaching lateral sides of segment 7 (Fig. 16B). Legs very long and slender; femur somewhat longer than tarsus; several basal segments in ♂

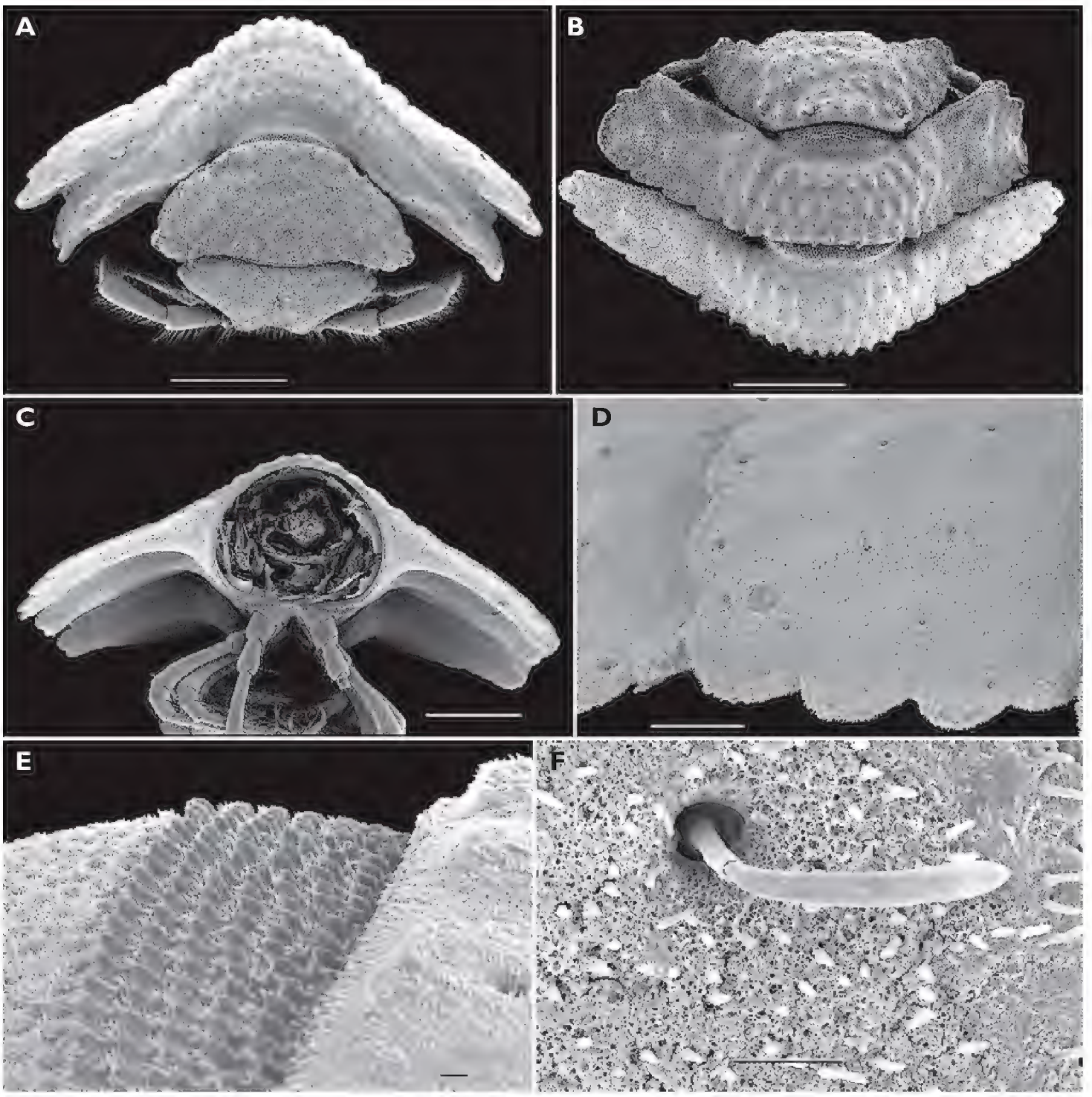

Figure 15. *Eutrichodesmus latus* sp. n., ♂ paratype from Yan Wu Dong Cave; **A** & **B**, anterior part of body, front and dorsal views, respectively; **C**, cross-section of segment 6, caudal view; **D**, midbody paratergum with ozopore; **E**, texture of prozonite and limbus; **F**, metatergal cerotegument with a bisegmented seta. – Scale bars: A, C, 0.5 mm, B, 0.2 mm, D, 0.1 mm, E, 0.02 mm & F, 0.01 mm.

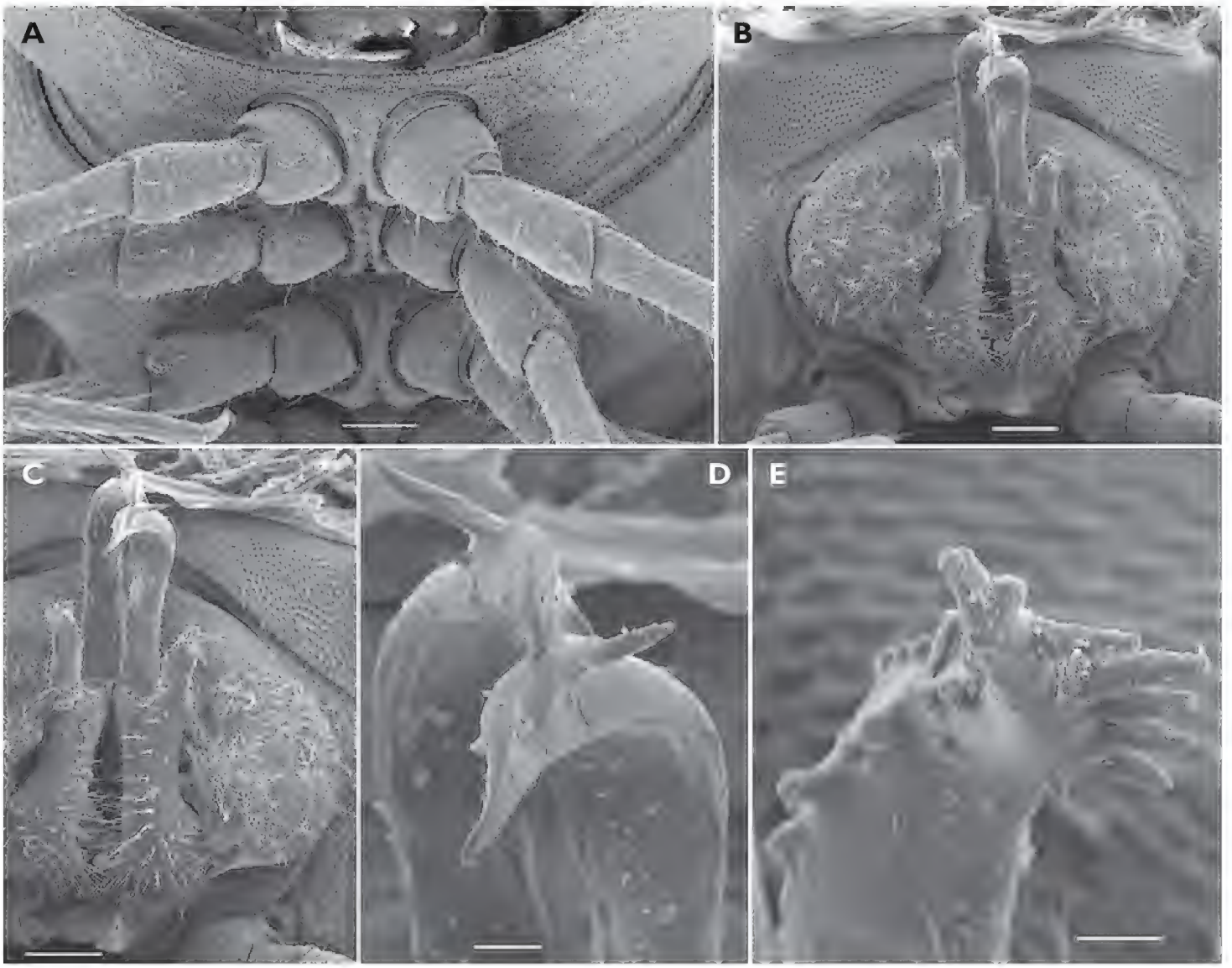

Figure 16. *Eutrichodesmus latus* sp. n., ♂ paratype from Yan Wu Dong Cave; **A**, midbody sterna, ventral view; **B**, gonopods, ventral view; **C**, same, ventral view; **D**, gonopod apices, ventral view; **E**, tip of distofemoral process of gonopods, ventral view. – Scale bars: A-C, 0.1 mm, D & E, 0.02 mm.

microtuberculate; claw simple, very slightly curved ventrad; some setae very sparsely microdenticulate (Figs 14F; 15C; 17A).

Gonopods (Figs 16B-E; 17B, C) very simple. Coxae subquadrate, large, microtuberculate and abundantly setose ventrolaterally, with a conspicuous triangular lobe frontolaterally. Telopodite considerably longer than coxite, slender, setose not only in its basal half but also at base of a digitiform and conspicuously microtuberculate distofemoral process (dp) situated laterally at about midway of telopodite, more distally with a slightly folded acropodite devoid of a hairpad; seminal groove terminating subapically.

Remarks. This species seems to be especially close to the next species.

***Eutrichodesmus similis* Golovatch, Geoffroy, Mauriès & VandenSpiegel, sp. n.**
urn:lsid:zoobank.org:act:9CE9BBFF-66DF-42BC-B4E8-C44E2C71F972
Figs 18-21.

Type material. China, Guangxi Prov., Mulun Nature Reserve, Gui Dong 2 Cave, 18.V.2007, leg. F. Bréhier (CHI-GX07-18/20), holotype ♂ (IZAS), paratypes: 2 ♂♂,

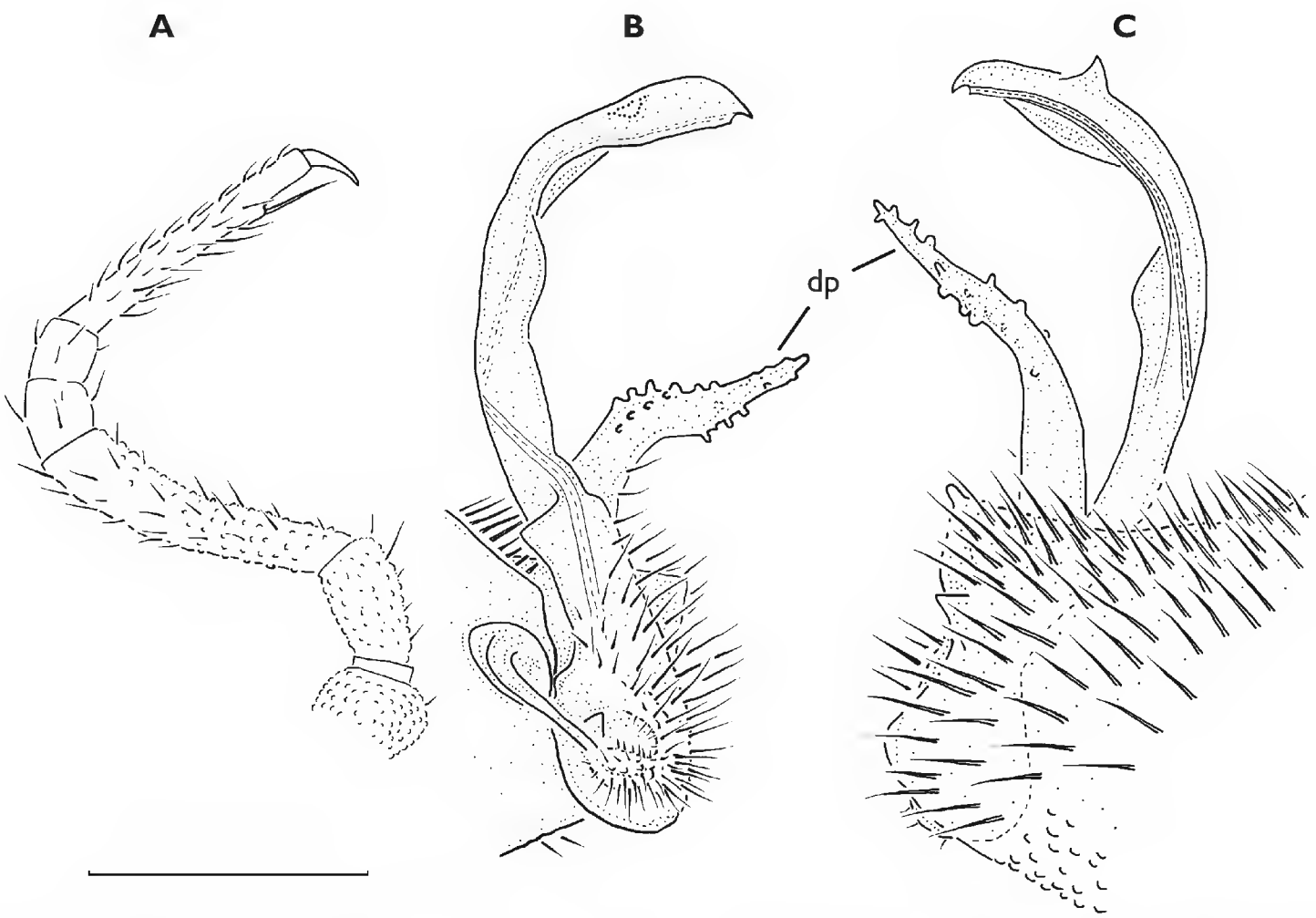

Figure 17. *Eutrichodesmus latus* sp. n., ♂ paratype from Yan Wu Dong Cave; **A**, leg 9; **B & C**, left gonopod, mesal and lateral views, respectively (dp = distofemoral process). – Scale bar: A, 0.1 mm; B & C, 0.2 mm.

2 ♀♀, 2 juv. (MNHN JC 313), 1 ♂, 1 ♀ (ZMUM), 1 ♂ (ZMUC), 1 ♂ (SEM); same locality, Shen Long Dong Cave, 22.V.2007, leg. L. Deharveng & A. Bedos (CHI-GX07-22/01); 1 ♂, 3 ♀♀, 4 juv. (SCAU).

Name. To emphasize the obvious similarities with the preceding species.

Diagnosis. See diagnosis of the previous species.

Description. Length of adults of both sexes *ca* 11-13 mm, width 3.0-3.3 mm; ♂♂ usually a little smaller than ♀♀. Holotype *ca* 12 mm long and 3.0 mm wide. Coloration uniformly pallid or light yellowish, only seldom marbled light-brownish.

All characters virtually as in *E. latus* sp. n. (Figs 18A-C, E, F; 19B-F; 20A, B), but collum with a row of very conspicuous teeth at front margin (Figs 18D; 19A).

Gonopods (Figs 20C, D; 21) slightly more complex than in *E. latus* sp. n. Telopodite distally somewhat expanded and folded, with a hairpad subapically.

Remarks. Together with *E. latus* sp. n., this remarkable species partly bridges the gap between "doratodesmoid" Haplodesmidae and the large tropical family Cryptodesmidae Karsch, 1879 in showing the very broad and, at most, only slightly declivous paraterga so characteristic of cryptodesmids, including those occurring in East and Southeast Asia (Hoffman 1980; Simonsen 1990). However, the metaterga in Cryptodesmidae are often densely setose, the collum is always enlarged, flabellate and covering the head from above to an even greater extent than it does in Pyrgodesmidae,

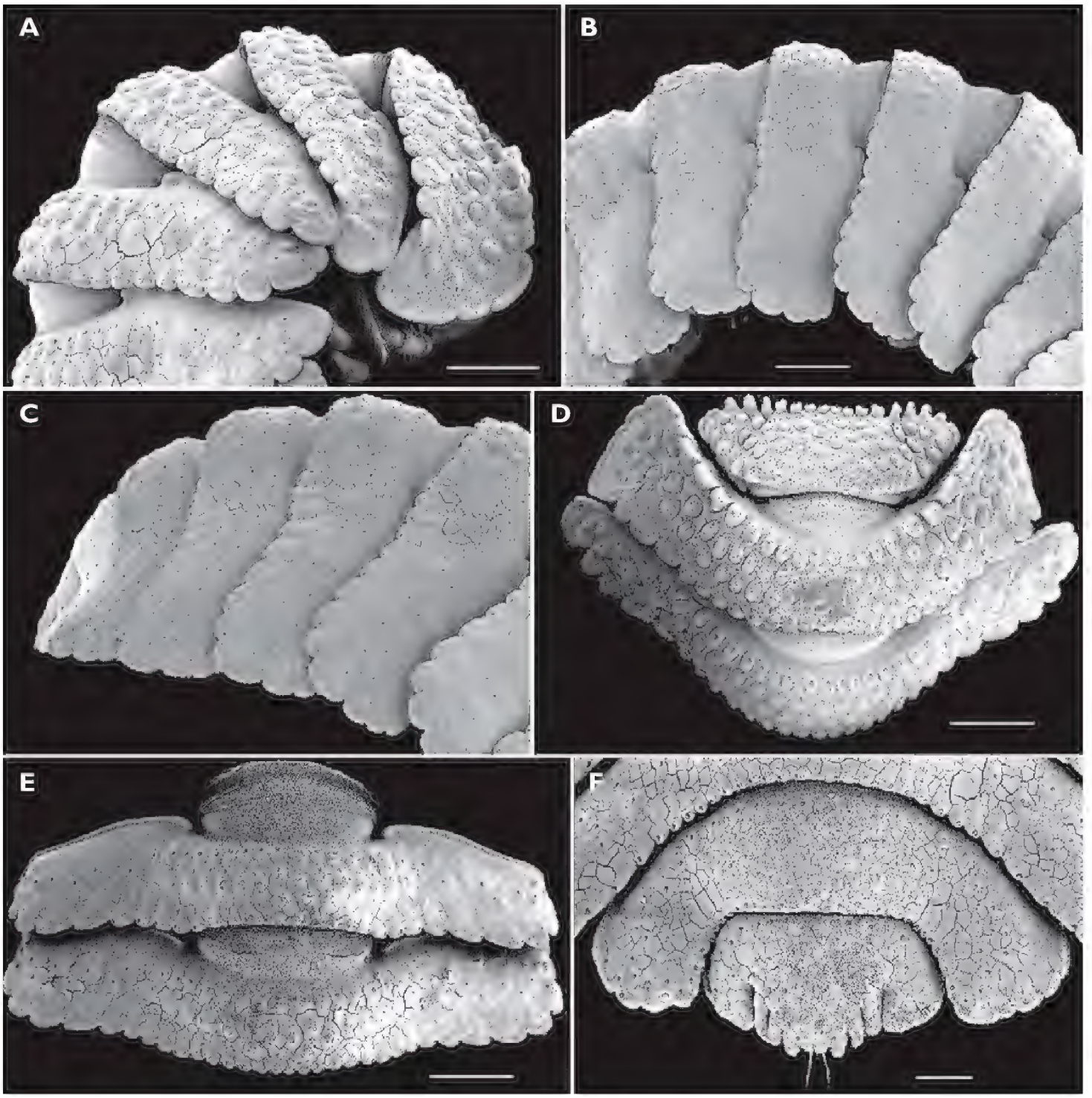

Figure 18. *Eutrichodesmus similis* sp. n., ♂ paratype from Gui Dong 2 Cave; **A**, anterior part of body, lateral view; **B**, midbody segments, lateral view; **C**, posterior part of body, lateral view; **D**, anterior part of body, dorsal view; **E**, midbody segments, dorsal view; **F**, posterior part of body, dorsal view. – Scale bars: A-E, 0.5 mm & F, 0.2 mm.

whereas the paraterga are often deeply incised caudolaterally or have clear radii, again much as in some Pyrgodesmidae. Therefore, it seems safe for the present to consider the Cryptodesmidae as a distinct family in the superfamily Polydesmoidea (Hoffman 1980, 1982b; Simonsen 1990).

What is more remarkable, however, is that the above two new Chinese species have the body so strongly flattened, and the paraterga apparently too broad to allow a tight volvation. This condition represents the opposite to that observed for *E. basalis* sp. n., in which the paraterga are obviously too short to permit complete volvation. In other words, within *Eutrichodesmus* we find species representing virtually the entire spectrum

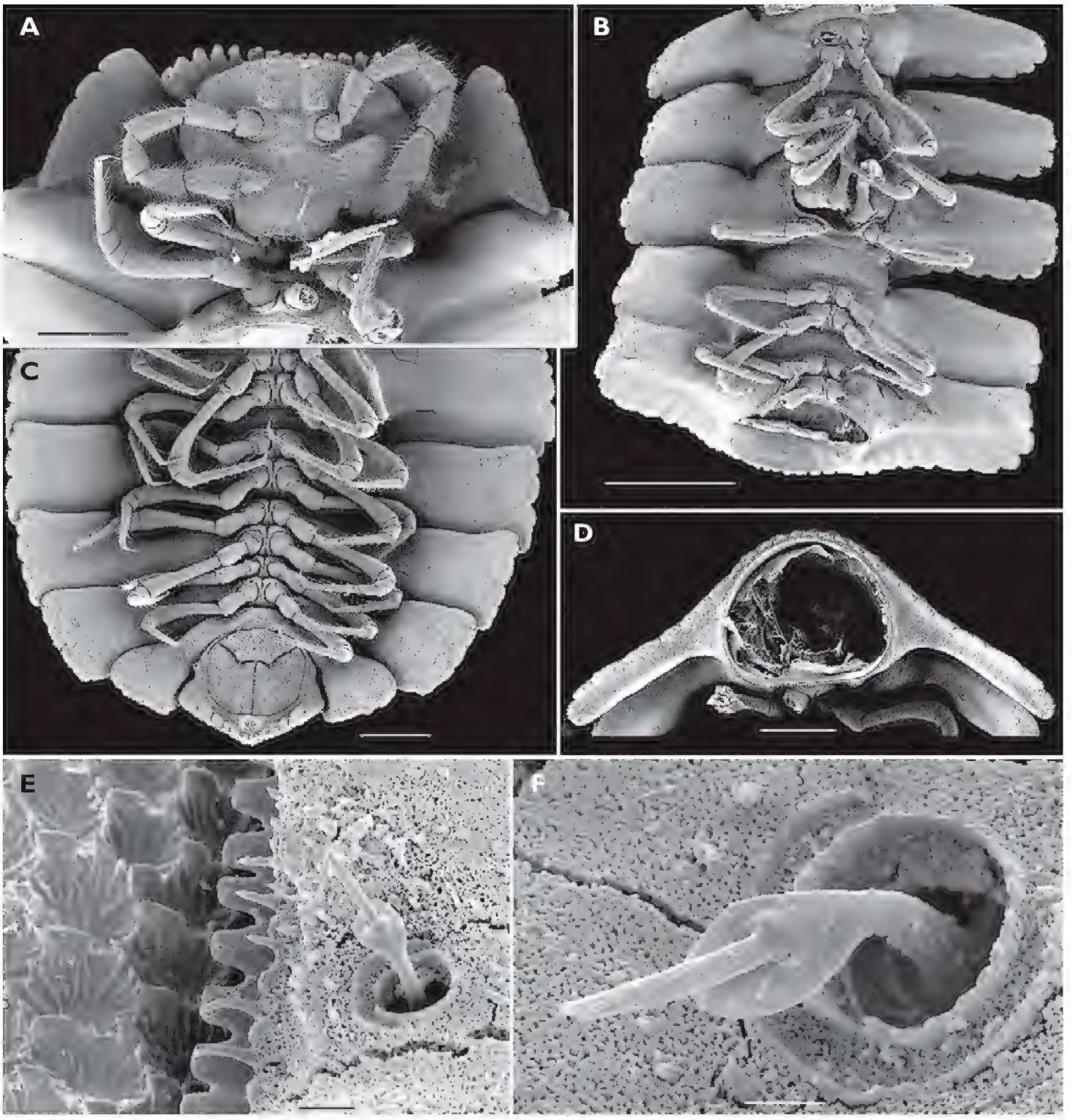

Figure 19. *Eutrichodesmus similis* sp. n., ♂ paratype from Gui Dong 2 Cave; **A**, anterior part of body, ventral view; **B**, segments 5-9, ventral view; **C**, posterior part of body, ventral view; **D**, cross-section of segment 4, caudal view; **E**, texture of prozonite, limbus and bisegmented seta; **F**, metatergal cerotegument with a bisegmented seta. – Scale bars: A, D, 0.5 mm, B, 1.0 mm, C, 0.02, E, 0.01 mm & F, 0.005 mm.

of "doratodesmid" evolution of conglobation, including a few exceptional cases of imperfect volvation.

Concerning the two new Chinese species that are not capable of complete conglobation, the situation somewhat parallels that observed in *Proeilodesmus mecistonyx* Hoffman, 1990 (Sphaeriodesmidae Humbert & DeSaussure, 1869, Sphaeriodesmoidea), a cavernicole from Mexico that is apparently incapable of volvation (Hoffman 1990). In contrast to "doratodesmids", however, most of the characters of this millipede seem plesiomorphic and suggest a link between a presumed flat-bodied che-

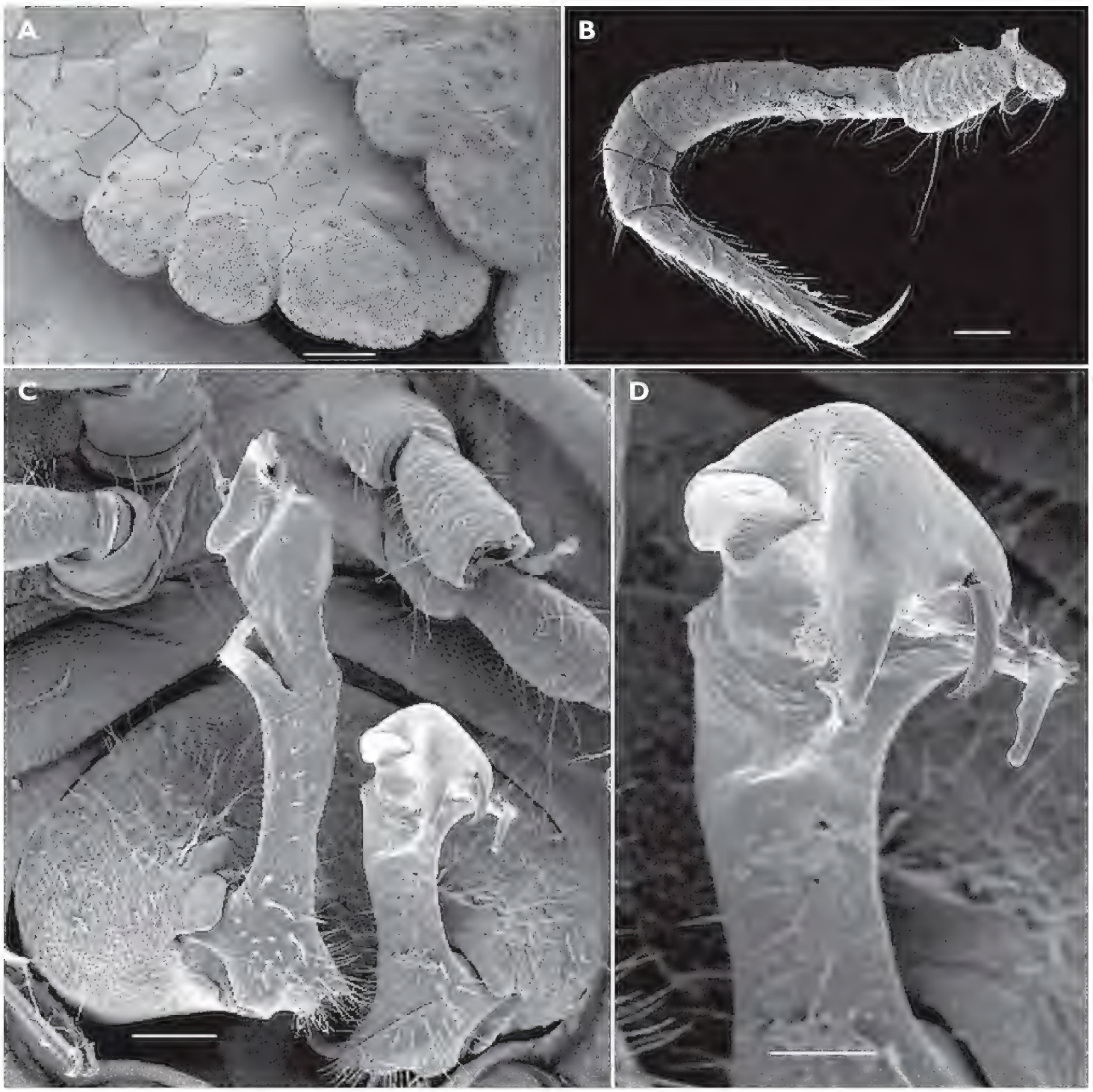

Figure 20. *Eutrichodesmus similis* sp. n., ♂ paratype from Gui Dong 2 Cave; **A**, paratergum with ozopore, lateral view; **B**, leg; **C**, gonopods, ventral view; **D**, gonopod apex, ventral view. – Scale bars: A-C, 0.1 mm & D, 0.05 mm.

lodesmidean (= leptodesmidean) ancestor and the remaining, convex, truly volvatory members of this rather large, Neotropical family (Hoffman 1990; Golovatch 2003).

***Eutrichodesmus incisus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, sp. n.**
urn:lsid:zoobank.org:act:4AF07ABA-62FA-4753-A991-B39D2E44146F
Figs 22-26.

Type material. China, Guizhou Prov., Qianxi County, Hong Lin Village, Tiao Shuz Dong Cave, 18.XI.2003, leg. L. Latella & G. Rossi, holotype ♂ (MNHN JC 314), paratypes: 1 ♂, 1 juv. (MNHN JC 314), 1 ♀ (SEM); same locality and cave,

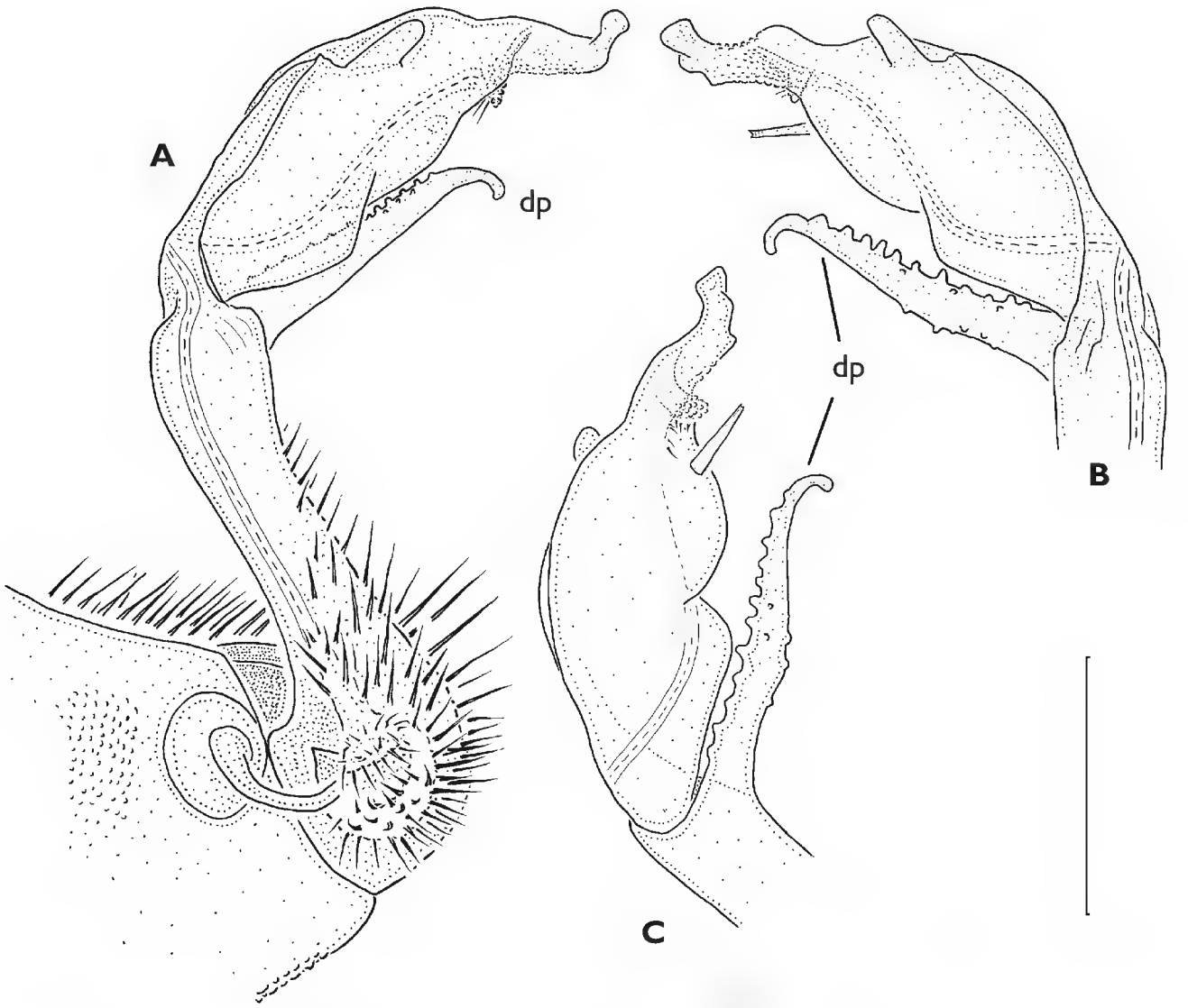

Figure 21. *Eutrichodesmus similis* sp. n., ♂ paratype from Gui Dong 2 Cave; **A**, left gonopod, mesal view; **B & C**, distal half of right gonopod, mesal and lateral views, respectively (dp = distofemoral process). – Scale bar: 0.2 mm.

18.XI.2003, leg. L. Latella, D. Avesani & G. Rossi, 1 ♂, 5 ♀♀, 1 juv. (MNHN JC 314), 2 ♀♀ (SCAU); same locality, Liao Jing Ling Dong Cave, 16.XI.2001, leg. L. Latella, 1 ♂, 1 ♀, 1 juv. (MCSNV), 1 ♀ (IZAS), 1 ♀ (ZMUM), 1 ♀ (ZMUC), 1 ♀ (MNHN JC 314), 1 ♂ (SEM); same locality, Shu Jia Yan Dong Cave, 16.XI.2001, leg. L. Latella & Berzacola, 1 ♀ (MNHN JC 314); same locality, Da Kong Dong Cave, 12.XI.2003, leg. L. Latella, 1 ♀ (MNHN JC 314); same locality, Luo Sai Dong Cave, 19.XI.2001, leg. D. Avesani, L. Latella & S. Meggiorini, 1 ♀ (MNHN JC 314).

Name. To emphasize the deeply incised caudolateral lobulations on most metaterga.

Diagnosis. Differs from all congeners by the unusually deeply incised caudolateral and lateral lobulations on most of the metaterga, as well as the peculiar, biramous, multituberculate, midway, lateral process (dp) of the gonopod telopodite.

Description. Length of adults of both sexes *ca* 7-8 mm, width 1.1-1.2 mm, body broadest at segments 3 and 4. Holotype *ca* 7 mm long and 1.2 mm wide. Coloration rather uniformly whitish to light yellow, anterior body parts often a little infuscate, light yellow-brownish.

Adults with 20 segments (Fig. 22A), conglobation pattern typical of "Doratodesmidae", complete. Head (Fig. 23B) basically as in preceding species, but tegument

slightly rougher (Figs 24A, B, D-F), antennae somewhat shorter (Fig. 23B), collum not covering head from above, regularly convex, with four rows of high, conical tubercles (Figs 22B, E). Metaterga behind collum with three transverse, rather regular rows of similarly high tubercles, most of which still retain very short, bisegmented setae (Fig. 22; 24E, F); limbus microcrenulate. Paraterga mostly directed ventrolaterad, strongly declivous, narrow, tips clearly surpassing the level of venter, unusually distinctly crenu-

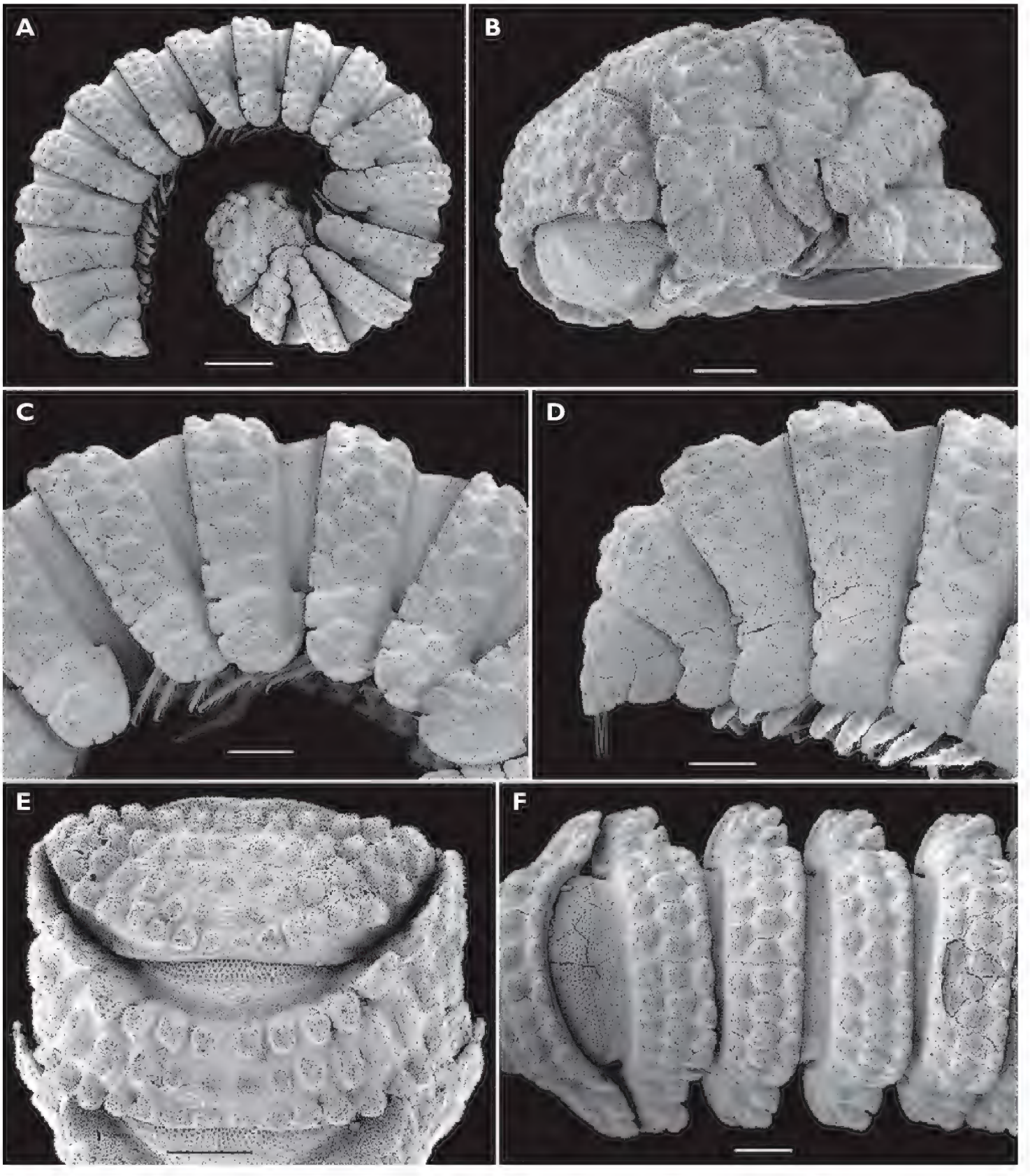

Figure 22. *Eutrichodesmus incisus* sp. n., ♀ paratype from Tiao Shuz Dong Cave; **A**, habitus, lateral view; **B**, anterior part of body, sublateral view; **C**, midbody segments, lateral view; **D**, posterior part of body, lateral view; **E**, anterior part of body, frontodorsal view; **F**, midbody segments, dorsal view. – Scale bars: A, 0.5 mm & B-F, 0.2 mm.

late/lobulate laterally and caudolaterally, usually with characteristic, deep incisions between lobules (Figs 22; 23E, F); paraterga 2 strongly enlarged, subvertical, anterolateral and lateral margins both evidently trilobate, caudal margin above schism with 4-5 similarly evident lobules, both schism and hyposchism small; paraterga 3 and 4 slightly shorter than others, bilobate laterally (Fig. 22B), following paraterga broadly rounded

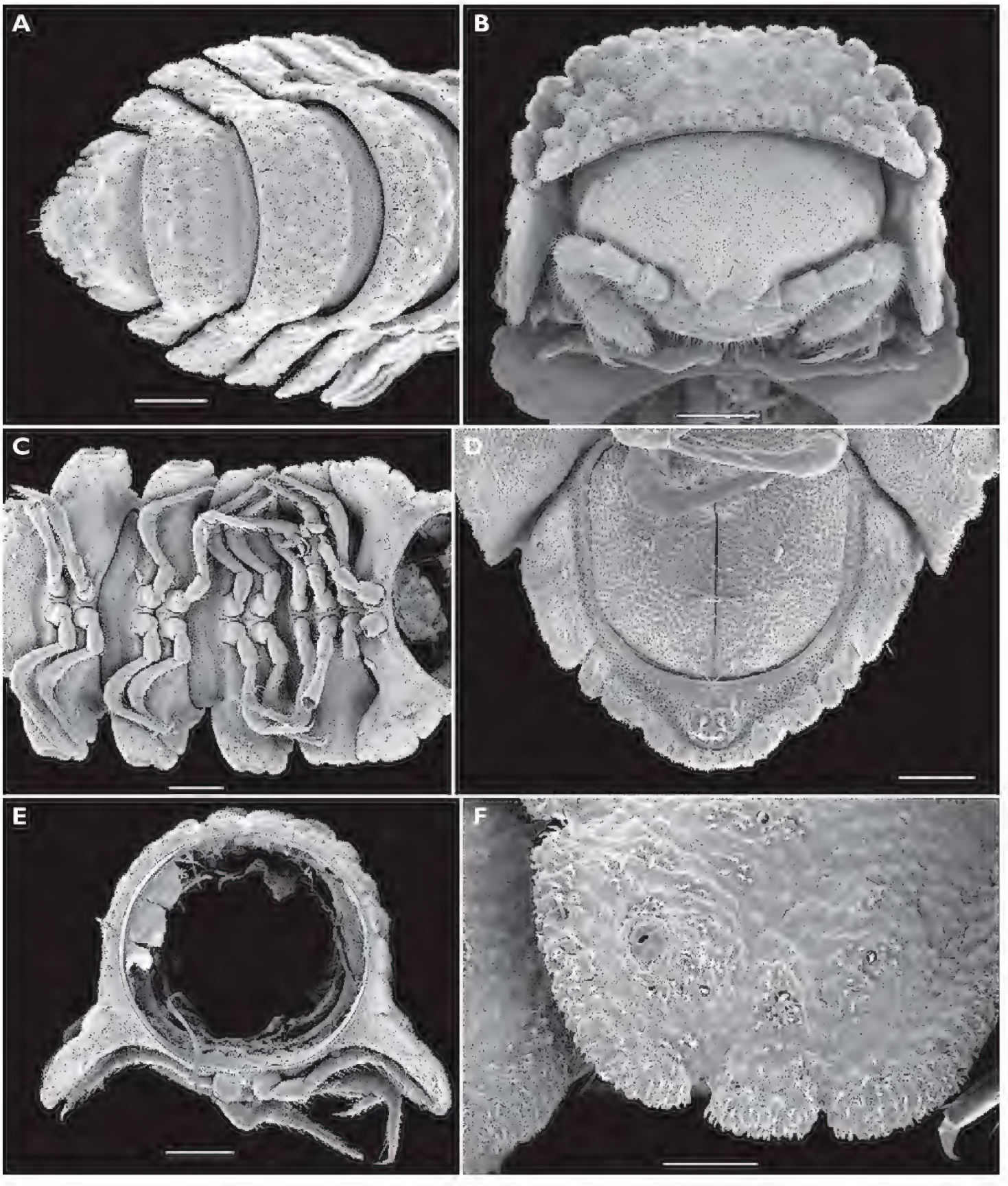

Figure 23. *Eutrichodesmus incisus* sp. n., ♀ paratype from Tiao Shuz Dong Cave; **A**, posterior part of body, dorsal view; **B**, anterior part of body, subventral view; **C**, midbody segments, ventral view; **D**, telson, ventral view; **E**, cross-section of a midbody segment, caudal view; **F**, paratergum with ozopore, lateral view. – Scale bars: A-C, E, 0.2 mm, D, 0.1 mm & F, 0.05 mm.

and mostly evidently trilobate, overlap typical. Pore formula normal, ozopores located near base of ventrocaudal lobulation (Fig. 23F). Pleurotergal carinae wanting. Epiproct strongly flattened, dorsally also tuberculate, with several deep incisions at lateral edge, directed ventrocaudad, with the usual four cones just below tip; para- and hypoprocts as in Figs 23A, D.

Sterna usually with a rather deep, narrow depression between coxae (Fig. 24C), only those between coxae 6, 7 and 9 much wider (Fig. 25A). Gonopod aperture transverse-

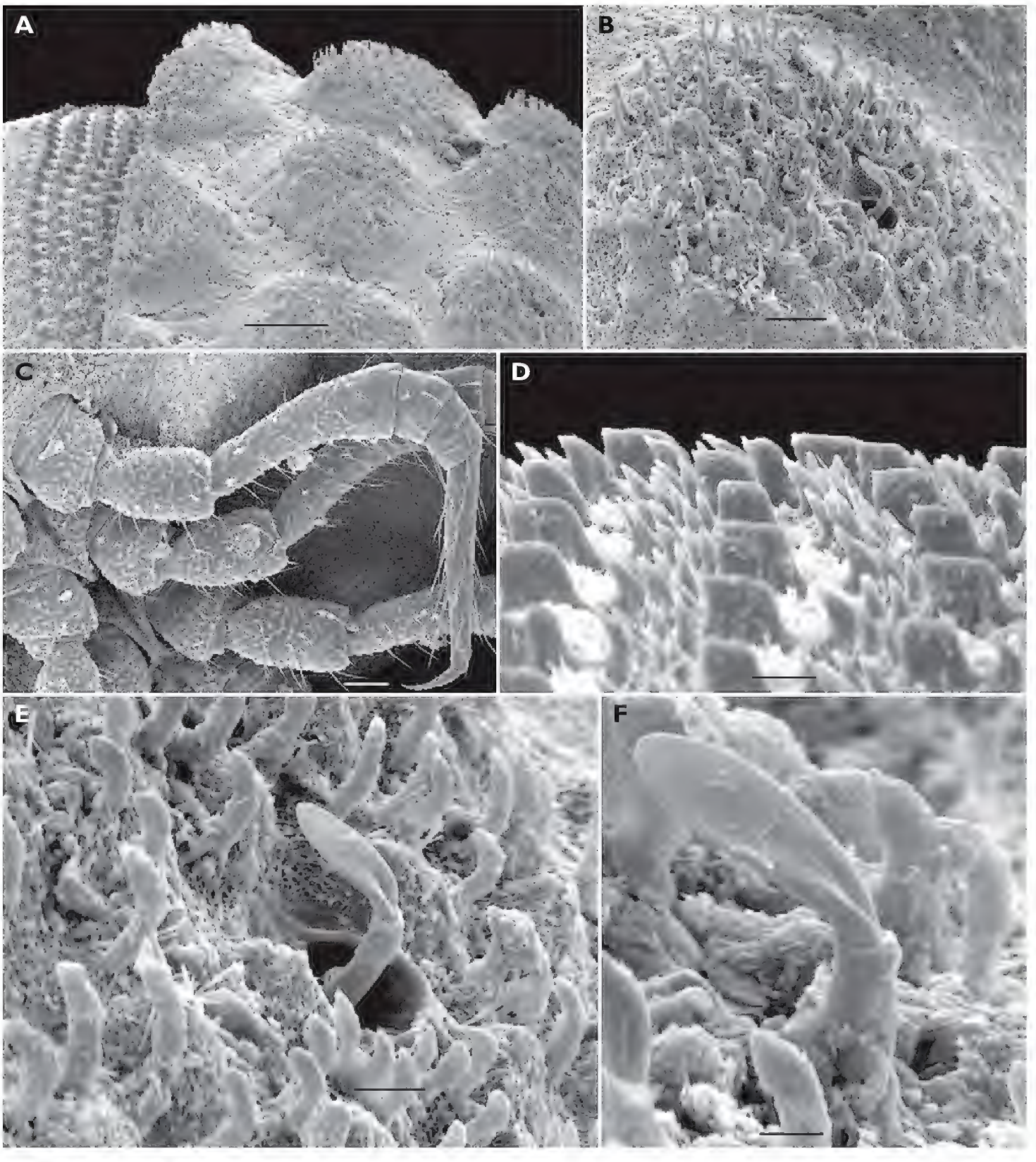

Figure 24. *Eutrichodesmus incisus* sp. n., ♀ paratype from Tiao Shuz Dong Cave; **A**, texture of pro- and metazona; **B**, texture of metatergal tubercle; **C**, midbody legs and sterna, ventral view; **D**, microtexture of prozonum, sublateral view; **E**, microvilli and a bisegmented seta; **F**, same enlarged. – Scale bars: A, C, 0.05, B, 0.01, D, E, 0.005 mm & F, 0.002 mm.

oval, relatively small, far from reaching lateral sides of segment 7. Legs rather short; femoral and tarsal segments equal and longest; several basal segments microtuberculate; claw simple, slightly curved ventrad; some setae very sparsely microdenticulate (Fig. 24C).

Gonopods (Figs 25A, B) relatively complex. Coxae subquadrate, large, microtuberculate and abundantly setose ventrolaterally, with a conspicuous triangular lobe frontola-

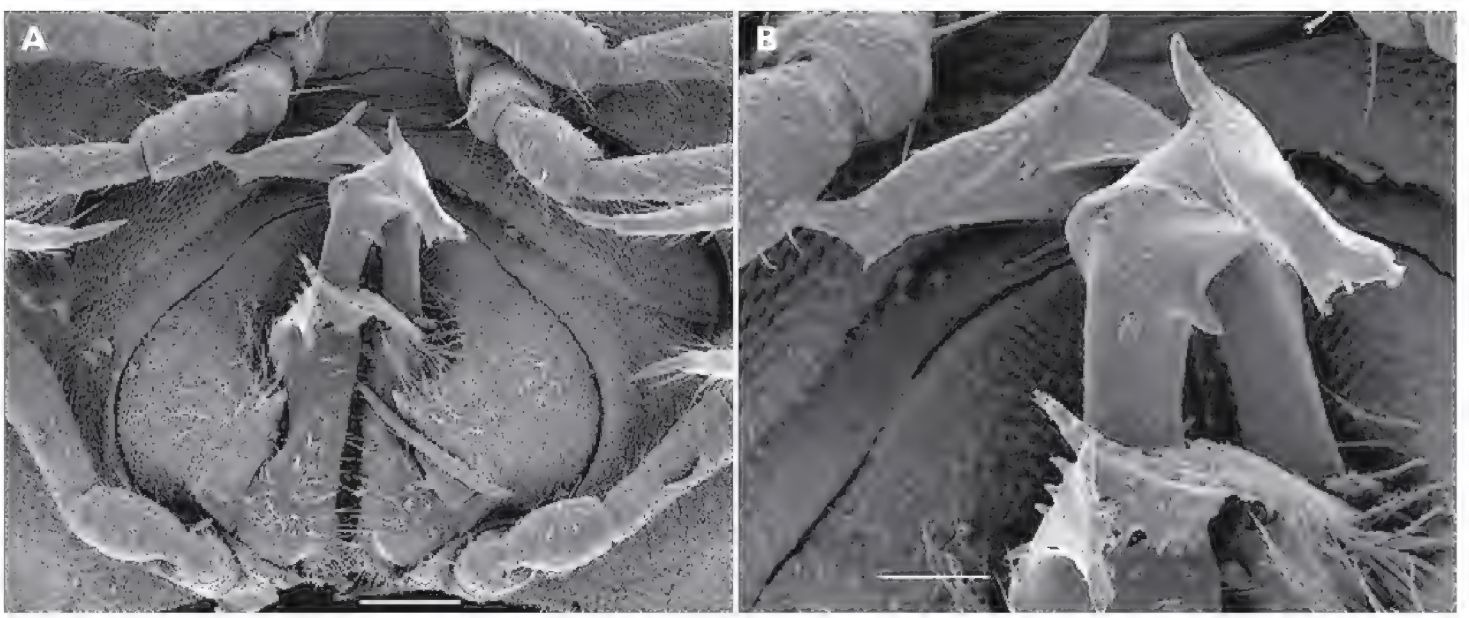

Figure 25. *Eutrichodesmus incisus* sp. n., ♂ paratype from Liao Jing Ling Cave; **A**, gonopods, ventral view; **B**, distal parts of gonopods, ventral. – Scale bars: A, 0.1 mm & B, 0.05 mm.

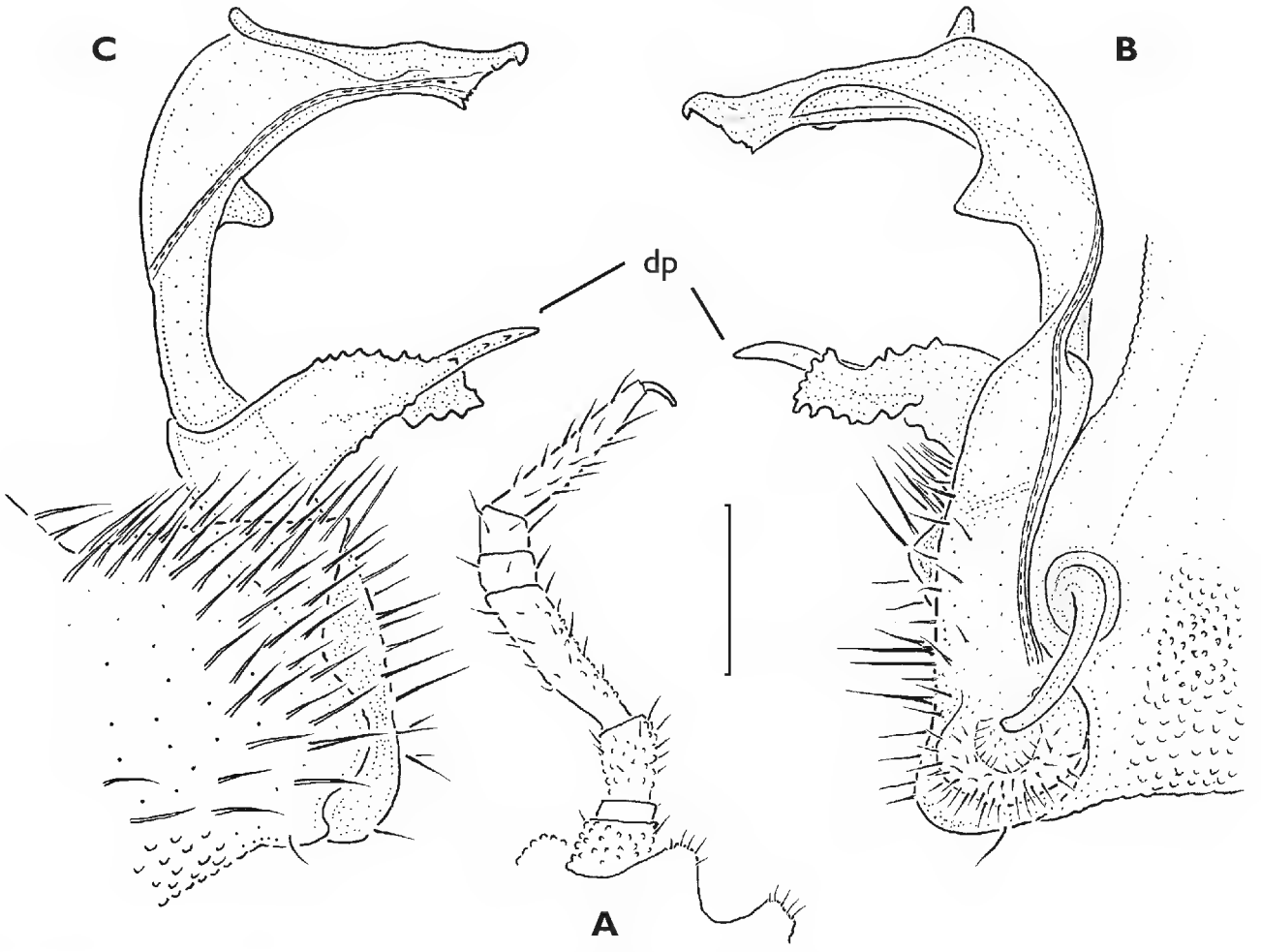

Figure 26. *Eutrichodesmus incisus* sp. n., ♂ paratype from Tiao Shuz Dong Cave; **A**, leg 9, caudal view; **B & C**, right gonopod, mesal and lateral views, respectively (dp = distofemoral process). – Scale bar: A, 0.2 mm, B, C, 0.1 mm.

terally. Telopodite considerably longer than coxite, unciform, rather slender, setose in its basal half, with a conspicuous, biramous, microtuberculate, distofemoral process (dp) laterally at about midway, more distally with a slightly folded acropodite bearing several small outgrowths, but devoid of a hairpad; seminal groove terminating subapically.

Remarks. *Glyphiulus latellai* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2007 is another millipede recorded from Tiao Shuz Dong and Shu Jia Yan caves (Golovatch et al. 2007a), whereas Liao Jing Ling Dong Cave contains the subcosmopolitan *Oxidus gracilis* (C. L. Koch, 1847) (Geoffroy and Golovatch 2004).

Doratodesmus grandifoliatus (Zhang *in* Zhang & Wang, 1993) n. comb.

Figs 27-30.

Material. China, Yunnan Prov., Mengzi County, pothole no. 2 (Ma Fa Tiao Dong), 6.I.1989, leg. P. Beron, 2 ♂♂, 1 ♀ (MNHN JC 315), 1 ♂, 3 ♀♀, 9 juv. (NMNHS), 1 ♂ (ZMUM), 1 ♀ (SEM); Yunnan Prov., Mengzi County, Longbaopo Dong Cave, 27.XI.1995, leg. I. Kos, B. Sket & F. Velkovrh, 1 ♂ & 1 ♀ *in copula* (OBBFUL), 1 ♂ (ZMUC), 1 ♂ (SEM).

Diagnosis. Differs from congeners by the simultaneous lack of mid-dorsal outgrowths on metaterga and of lateral lobulations on paraterga 2, the presence of deep crenulations at the caudal edge of most metaterga, coupled with a peculiar shape of the gonopod telopodite supplied with a large, multidenticulate, lateral lobe and a long, slightly curved, rather simple acropodite.

Short redescription. Length of adults of both sexes *ca* 10-11 mm, width 1.8-2.1 mm, body broadest at segments 3 and 4. Coloration rather uniformly whitish to light yellow, anterior body parts often a little infuscate, light yellowish-brown.

Adults with 20 segments, conglobation pattern typical of "Doratodesmidae", complete (Golovatch 2003). Superficially, strongly resembling *Eutrichodesmus incisus* sp. n.

All characters fully agreeing with the original description (Zhang and Wang 1993), but augmented here by illustrations showing more details: head (Fig. 28C), antennae (Fig. 28C, D), collum (Fig. 27D), meta- and paraterga (Figs 27A-C, E, F; 28B), tegument and tergal setae (Figs 28F; 29A, B), ozopores (Fig. 28E), telson (Fig. 27F; 28A), legs (Figs 29C, D; 30A).

Sterna usually with a rather deep, narrow depression between coxae (Fig. 28B), only those between coxae 6, 7 and 9 much wider (Fig. 30A). Gonopod aperture transverse-oval, relatively small, far from reaching lateral sides of segment 7. Legs rather long; femoral and tarsal segments equal and longest; several basal segments microtuberculate; claw simple, slightly curved ventrad; some setae sparsely microdentate (Figs 29C, D; 30A).

Gonopods (Figs 30B, C) relatively complex. Coxae subquadrate, large, microtuberculate and abundantly setose ventrolaterally. Telopodite considerably longer than coxite, subunciform, basal half slender and setose, at about midway conspicuously enlarged, with a multidenticulate lateral lobe (lo) and a very short solenomere (sl) with a hairpad on top; acropodite relatively long and simple.

Remarks. This species has hitherto been described or reported from three caves in Yunnan, China (Wang and Zhang 1993; Golovatch 2003). One of the new samples (from Longbaopo Cave) is strictly topotypic, while Ma Fa Tiao Dong Cave is known to support another millipede, *Glyphiulus subgranulatus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2007 (see Golovatch et al. 2007a).

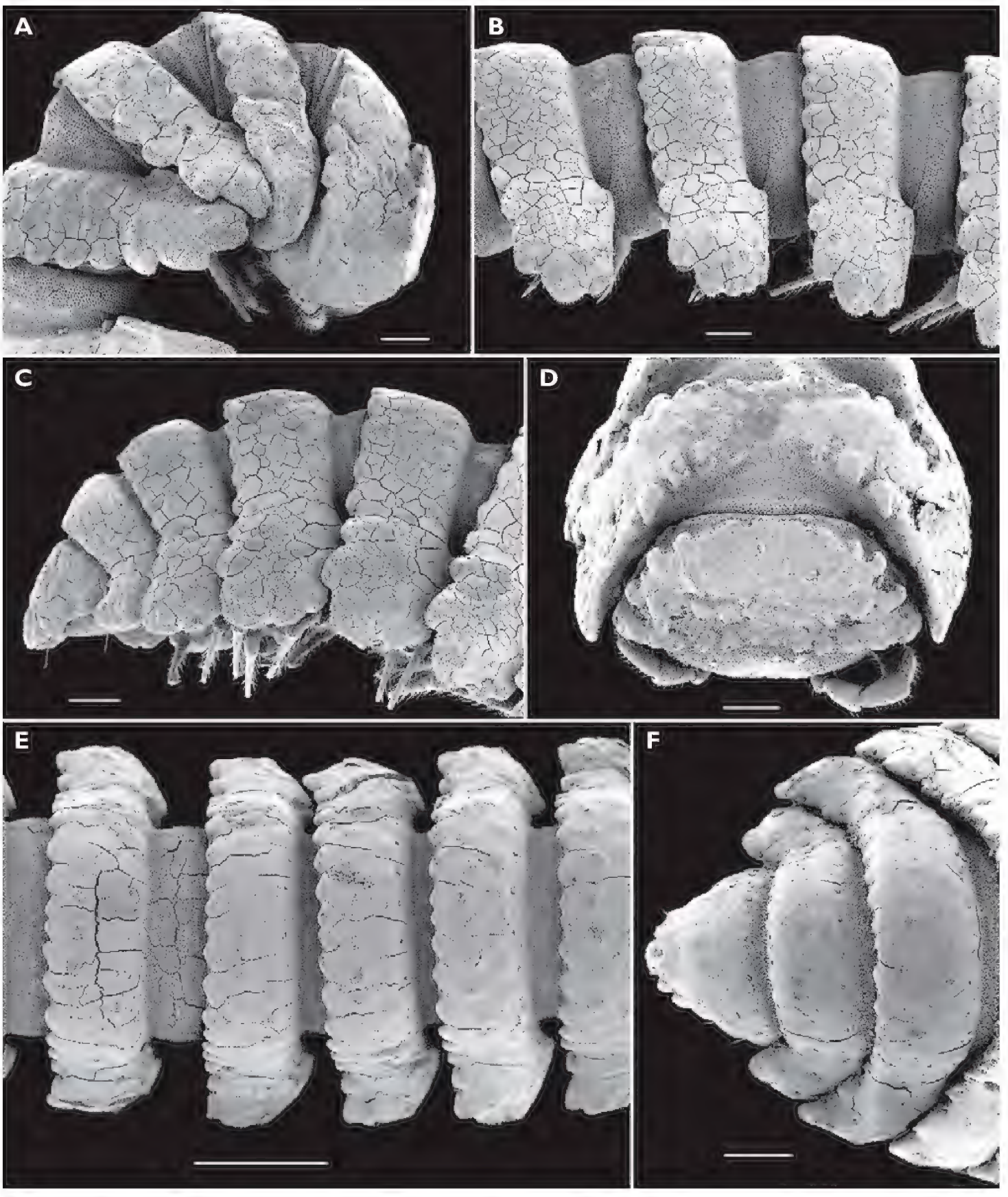

Figure 27. *Doratodesmus grandifoliatus* (Zhang *in* Zhang & Wang, 1993), ♀ from Longbaopo Dong Cave (A-C) and ♀ from Ma Fa Tiao Dong Cave (D-F); **A**, anterior part of body, lateral view; **B**, midbody segments, lateral view; **C**, posterior part of body, lateral view; **D**, anterior part of body, frontodorsal view; **E**, midbody segments, dorsal view; **F**, posterior part of body, dorsal view. – Scale bars: A-D, F, 0.2 mm & E, 0.5 mm.

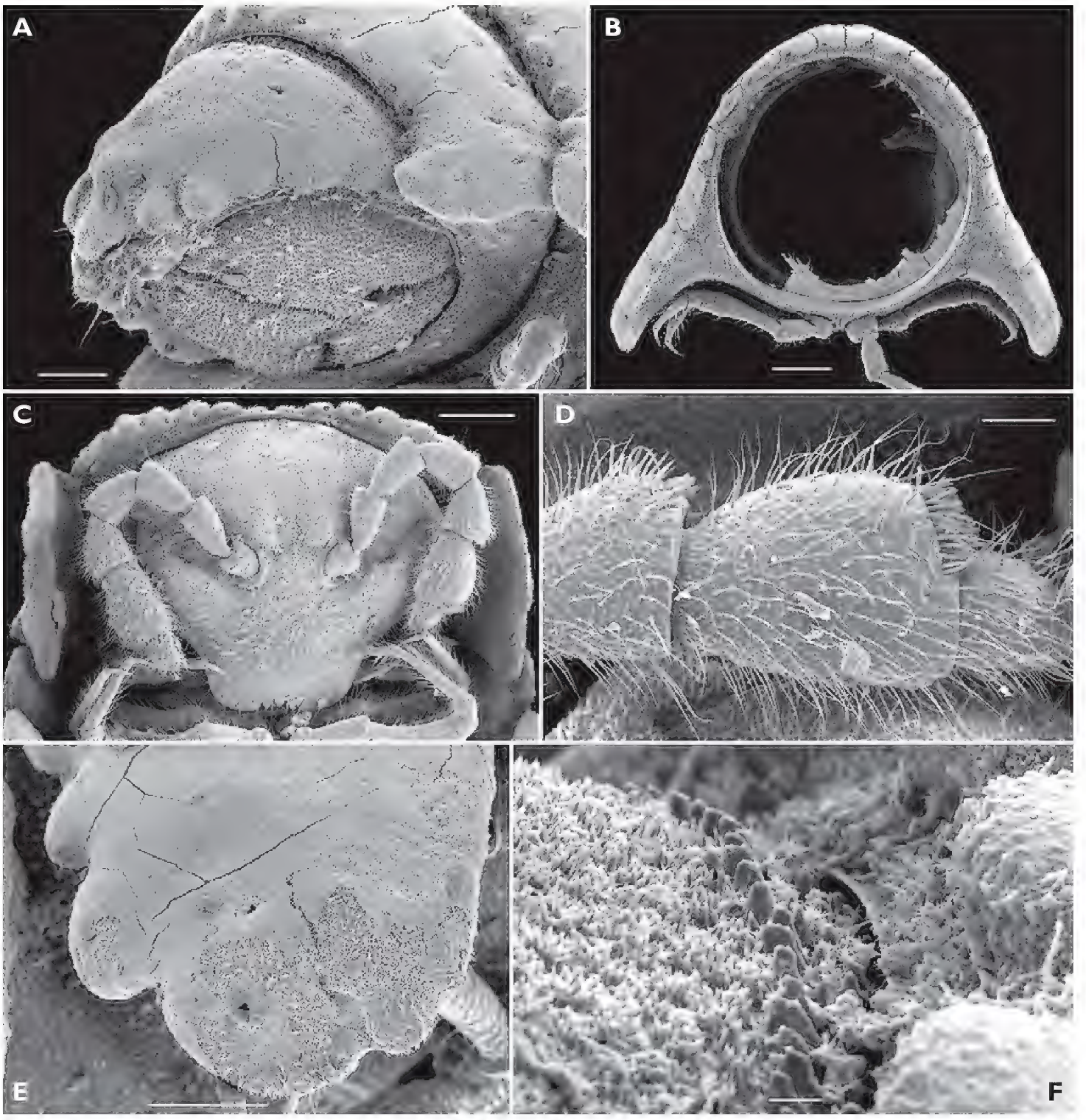

Figure 28. *Doratodesmus grandifoliatus* (Zhang *in* Zhang & Wang, 1993), ♀ from Ma Fa Tiao Dong Cave; **A**, telson, ventrolateral view; **B**, cross-section of a midbody segment, caudal view; **C**, head, front view; **D**, distal part of antenna; **E**, paratergum with ozopore, lateral view; **F**, tegument, sublateral view. – Scale bars: A, E, 0.1 mm, B, C, 0.2 mm, D, 0.05 mm & F, 0.01 mm.

Discussion

Concerning the generic reclassification of the Haplodesmidae s.l., which is consistently based on male gonopod characters alone, only very few genera can be distinguished, arranged in two major grades. The basalmost grade can be termed "haplodesmid", comprising the species that are completely incapable of volvation. Their paraterga are either rudimentary or too short to allow a sufficiently tight body enrollment to conceal the legs.

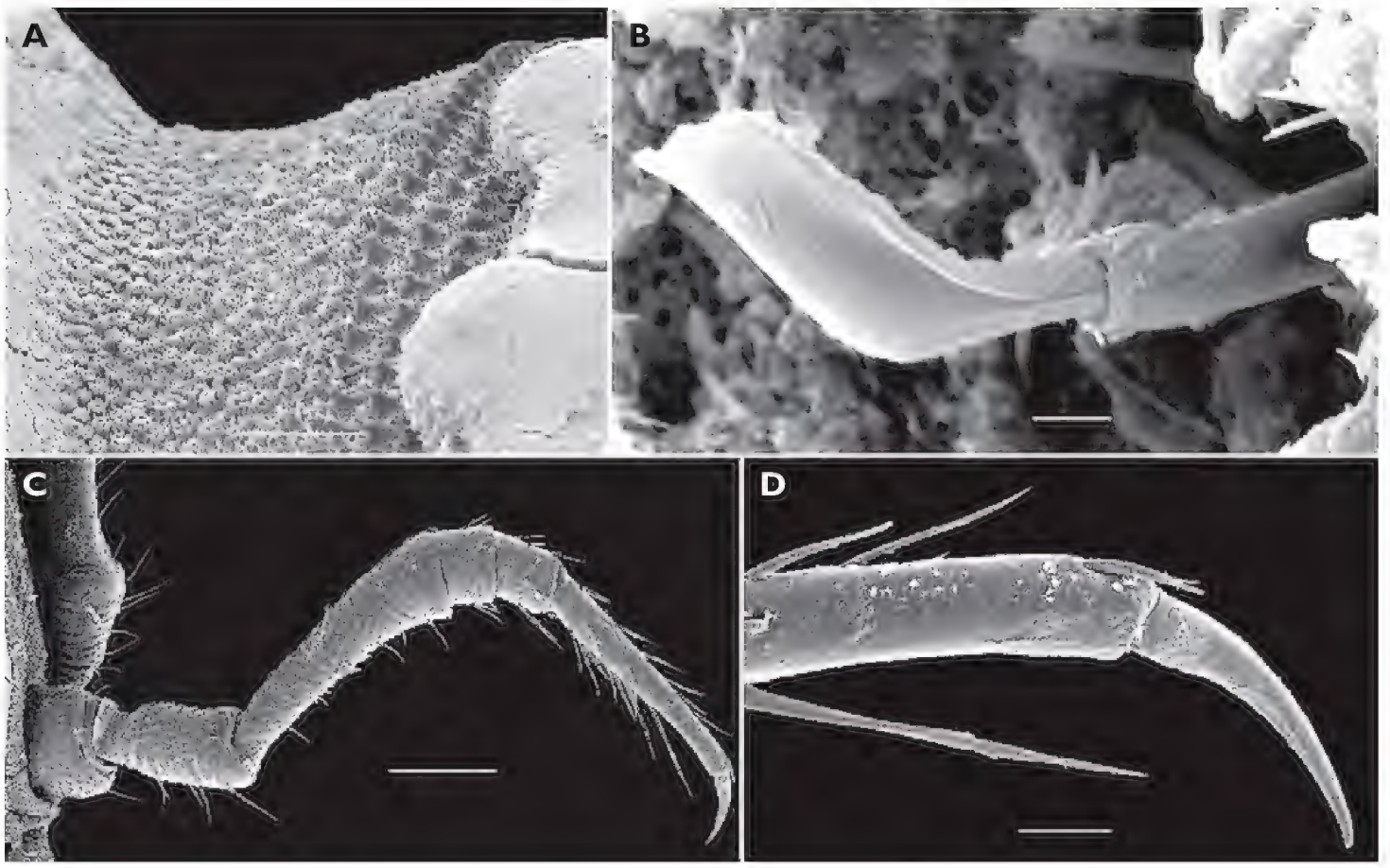

Figure 29. *Doratodesmus grandifoliatus* (Zhang *in* Zhang & Wang, 1993), ♀ from Ma Fa Tiao Dong Cave; **A**, texture of pro- and metazona; **B**, bisegmented seta; **C**, leg and sternum, caudal view; **D**, claw. – Scale bars: A, 0.05 mm, B, 0.002 mm, C, 0.1 mm & D, 0.02 mm.

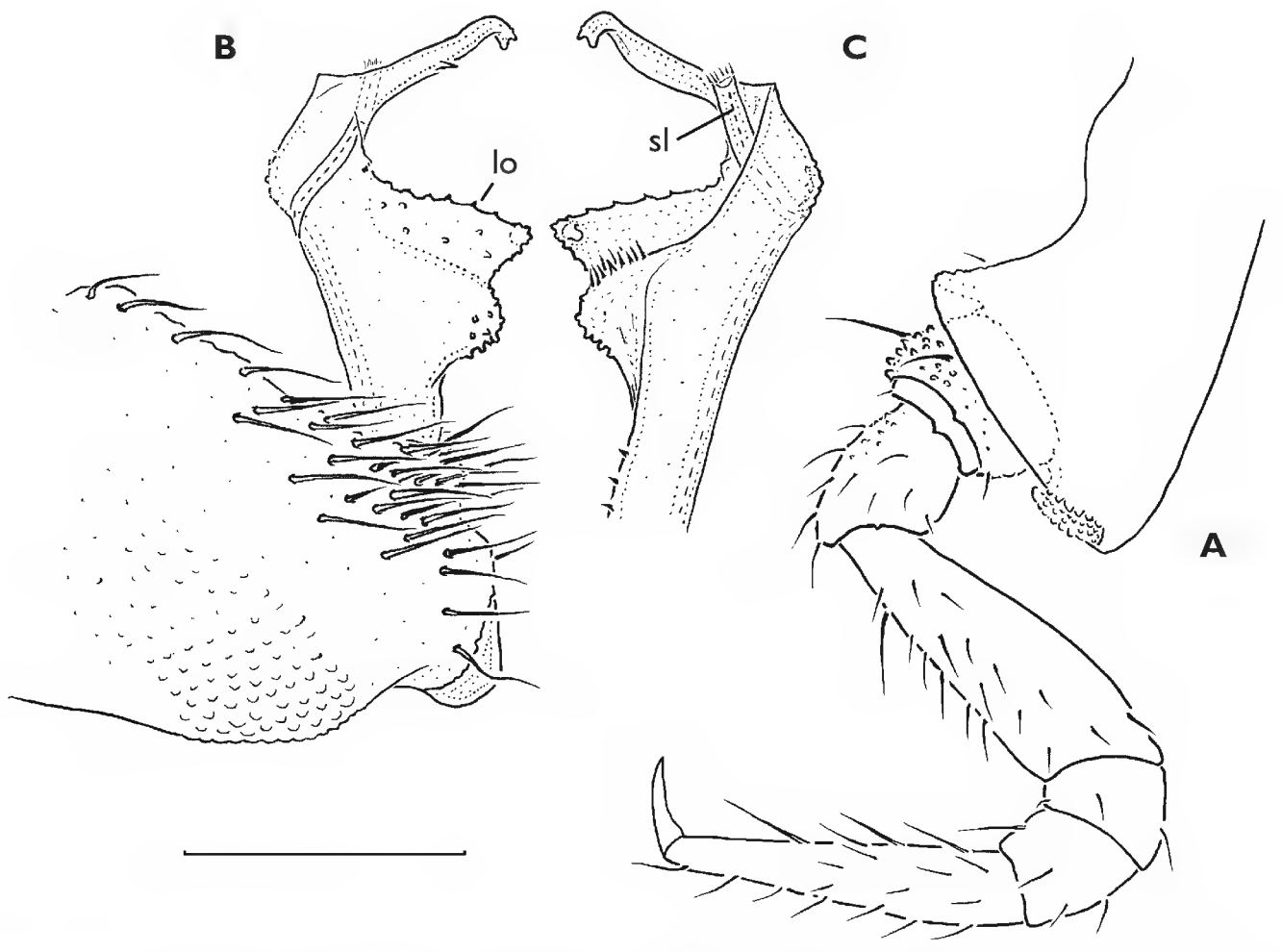

Figure 30. *Doratodesmus grandifoliatus* (Zhang *in* Zhang & Wang, 1993), ♂ from Ma Fa Tiao Dong Cave; **A**, leg 9, caudal view; **B & C**, right gonopod, lateral and mesal views, respectively (sl = solenomere; lo = lateral lobe). – Scale bar: A, 0.2 mm, B, C, 0.1 mm.

The basalmost genus seems to be *Prosopodesmus* Silvestri, 1910 (= *Homodesmus* Chamberlin, 1918) (see Hoffman 1980), because it still retains rather well-developed paraterga, including somewhat enlarged paraterga 2 and porosteles, as well as gonopods of the same type as in Polydesmidae (Polydesmoidea). The pyrgodesmid-like body could further have become either subcylindrical – due to the loss of most paraterga, leading to the few completely vermiform haplodesmids – or enlarged, more elaborate and leading to the "doratodesmids" already capable of volvation. The gonopods of *Prosopodesmus* show only a few setae on the coxa, the telopodite is rather simple, slender, basically uniramous and falcate, with or without a more or less pronounced midway (= distofemoral) outgrowth; the femorite is rather long and slender, with evidence of torsion in its distalmost part, because the seminal groove terminates much more distally on a short lobe with a hairpad on top after a shift laterad near the end of the femorite; a simple acropodite distal to the hairpad is of considerable size and indistinctly dentate. As in all Polydesmoidea (Polydesmidae, Cryptodesmidae and Haplodesmidae), the gonopod aperture is modest in size and transverse-ovoid; the gonocoxae are subquadrate, non-globose and enlarged laterally; the telopodites are held parallel to the main axis, barely crossing each other, if at all, even distally, but hinging into a considerable hollow formed by the ventromedian parts of the coxae. The adjacent male coxae are broadly separated by an extended and elevated caudal edge of the gonopod aperture (leg 9) and to receive the end parts of the gonopods (leg 7 or legs 6 and 7).

Both pyrgodesmid-like Haplodesmidae – *Prosopodesmus* and *Rhipidopeltis* Miyosi, 1958 – share the flabellate collum covering the head from above, the evident, declivous and trilobate paraterga, the tuberculate metaterga (with the tubercles arranged in three transverse rows) and, above all, a very similar gonopod structure. Thus, the telopodites are simple, subfalcate, modestly elongated and devoid of a separate solenomere branch. Since the differences in the position of the orifice of the seminal groove (distal with a hairpad in *Prosopodesmus*, terminal without hairpad in *Rhipidopeltis*) are here considered to be only species-specific, we do not hesitate to formally synonymize these genera and make the following nomenclatural changes: *Prosopodesmus* Silvestri, 1910 = *Rhipidopeltis* Miyosi, 1958, n. syn., and *Prosopodesmus sinuatus* (Miyosi, 1958), n. comb.

Although the monobasic genus *Hyperothrix* Attems, 1900, from the Seychelles (Attems 1900), has sometimes been placed close to, or within, Doratodesmidae (e.g. Hoffman 1982a), based on the gonopod structure alone, we consider it to be a disjunct Pyrgodesmidae quite remote from Haplodesmidae (Golovatch 2003). Similarly, the small genus *Hypsiloporus* Loomis, 1961, from Panama is quite different from all haplodesmids and seems best transferred to Fuhrmannodesmidae Brolemann, 1916, as suggested by Hoffman (1999).

The following stages in the development of a vermiform body are distinguished among haplodesmids. Each is here allotted the rank of a genus and characterized by its degree of gonopod regression (simplification).

Cylindrodesmus Pocock, 1889 (see complete review by Golovatch et al. 2001) seems to be more aberrant, characterized by gonocoxae which are only relatively poorly setose on the ventrolateral surface, and particularly simple telopodites, either strictly

uniramous (= solenomere alone) or biramous (= solenomere and a midway process), with the seminal groove terminating apically and devoid of a hairpad.

Superficially, *Cylindrodesmus* is characterized by a particular, very dense and mixed trichome, consisting of long simple setae and even longer, bisegmented tactile setae (Golovatch et al. 2001). However, like porosteles, bisegmented setae (albeit often rudimentary) appear sporadically throughout the Haplodesmidae. Moreover, they are not restricted to this family alone, also occurring in some quite remote groups of Diplopoda, such as the small Australian genus *Australeuma* Golovatch, 1986 (Chordeumatida: Metopidiotrichidae Attems, 1907) (Shear and Mesibov 1997). Yet there can be no doubt that the polydesmoid ancestor of Haplodesmidae must have had bisegmented setae and porosteles.

Another disjunct member of Haplodesmidae is *Helodesmus* Cook, 1896 (see Hoffman 1964, 1980), a genus characterized by relatively poorly setose gonocoxae and a considerably shortened prefemoral+femoral (= setose) portion of the telopodite, deeply biramous thereafter, with a long and flagelliform solenomere devoid of a hairpad. *Atopogonus* Carl, 1926 is yet another aberrant genus, unusual in showing virtually bare and reduced gonocoxae and peculiar, strongly geniculate telopodites, coupled with no traces of either a coxal cannula or a seminal groove (Carl 1926; Jeekel 1986).

Since the type species of *Agathodesmus Silvestri*, 1910 is a *nomen inquirendum*, nothing can be said about its identity (see above).

At the other extreme, along with a progressive development of paraterga, especially strongly enlarged paraterga 2 and a correlated size decrease of the collum, the pyrgodesmid-like (but actually polydesmoid!) ancestor of Haplodesmidae could have given rise to the "doratodesmid" grade, most species of which are capable of volvation. The volvation pattern appears to be characteristic of the entire grade, i.e. paraterga 2-4(5) each with a small caudolateral hyposchism for laterally receiving the anterolateral, usually shortened part of the next paratergum. Thereafter the pattern changes to typical, with the anterior portion of each paratergum placed beneath the caudal margin of the previous one (Golovatch 2003). Despite the striking variety of peripheral characters (often with peculiar mid-dorsal projections, metatergal lobulations, tuberculations etc.), there seem to be only two distinguishable species groups, each considered as warranting generic rank.

The genus *Doratodesmus* Cook *in* Cook & Collins, 1895 can be diagnosed by the gonopod coxae usually being abundantly setose ventrolaterally, the telopodite usually quite stout, strongly enlarged laterally towards the end of the femorite, with or without a short solenomere branch thereafter; the acropodite is variable, from absent to well-developed. Since this set of characters is observed in several "doratodesmids", the following new synonymies and combinations are proposed: *Doratodesmus* Cook *in* Cook & Collins, 1895 = *Pauroplus* Chamberlin, 1945, = *Eucondylodesmus* Miyosi, 1956, = *Scolopopyge* Hoffman, 1978, = *Selminarchus* Hoffman, 1978, = *Crenatidorsus* Zhang *in* Zhang & Wang, 1993 (all n. syn.);

Doratodesmus elegans (Miyosi, 1956), *Doratodesmus grandifoliatus* (Zhang *in* Zhang & Wang, 1993), *Doratodesmus analdes* (Chamberlin, 1945), *Doratodesmus pholeter*

(Hoffman, 1978), *Doratodesmus hispidus* (Hoffman, 1978) (all n. comb.). This genus seems to be more advanced than the following, in which the gonopods more strongly resemble the presumed basal condition observed in *Prosopodesmus*.

The genus *Eutrichodesmus* Silvestri, 1910 can be diagnosed by the gonopod coxae often being abundantly setose ventrolaterally, the telopodite usually slender, not enlarged toward the end of the femorite, but with a more or less distinct process or outgrowth laterally, opposite the recurvature point of the seminal groove; the solenomere thereafter takes up most of the telopodite and is sometimes elaborate, with the seminal groove terminating distally to subapically, with or without a hairpad; the acropodite is small to nearly absent. Because this set of characters is shared by numerous "doratodesmids", the following new synonymies and combinations are proposed: *Eutrichodesmus* Silvestri, 1910 = *Ascetophacus* Hoffman, 1977, = *Cerastelachys* Hoffman, 1977, = *Dimorphodesmus* Murakami, 1966, = *Dyomerothrix* Hoffman, 1982, = *Parapauroplus* Zhang, *in* Zhang & Wang, 1993, = *Pocillidorsus* Zhang, *in* Zhang & Wang, 1993 (all syn. n.); *Eutrichodesmus macclurei* (Hoffman, 1977), *Eutrichodesmus reclinatus* (Hoffman, 1977), *Eutrichodesmus cavernicola* (Sinclair, 1901), *Eutrichodesmus peculiaris* (Murakami, 1966), *Eutrichodesmus gremialis* (Hoffman, 1982), *Eutrichodesmus monodentus* (Zhang *in* Zhang & Wang, 1993), *Eutrichodesmus dorsiangulatus* (Zhang *in* Zhang & Wang, 1993) (all n. comb.). This is the largest genus of Haplodesmidae showing virtually the entire spectrum of conglobation capacities within the "doratodesmid" grade. We refrain from allotting any taxonomic rank to the two grades, regarding them instead as opposite evolutionary trends.

The new generic classification of Haplodesmidae can be summarized as follows.

Family Haplodesmidae Cook, 1895

Type genus: *Haplodesmus* Cook, 1895 (replacement name for the preoccupied *Haplosoma* Verhoeff, 1894).

= Haplosomidae Silvestri, 1895. Type genus: *Haplosoma* Verhoeff, 1894.

= Doratodesmidae Cook, 1896, n. syn. Type genus: *Doratodesmus* Cook *in* Cook & Collins, 1895 (replacement name for the preoccupied *Doratonotus* Pocock, 1894).

Diagnosis. A family of Polydesmoidea with gonopod aperture relatively modest in size, transverse-ovoid; gonocoxae subquadrate, non-globose, enlarged laterally, often densely setose; telopodites usually rather simple, uni-, bi- or triramous, usually with evidence of torsion near end of femorite, rather stout (about as high as coxae) to very slender, always held parallel to main axis, not crossing each other even distally, but hinging into a considerable hollow formed by ventromedian parts of coxae; seminal groove and coxal cannula usually present, solenomere only seldom being a separate branch (occasionally long and flagelliform), usually taking up much to most of telopodite distad of a more or less evident, lateral process, lobe or outgrowth near end of femorite, latter enlarged or slender; acropodite varying from very conspicuous to nearly absent.

Body shape ranging from vermiform/subcylindrical or "pyrgodesmid-like" (see Key below) (neither capable of volvation) to "doratodesmid" (capable of volvation). Paraterga, if present, always declivous, hence the dorsum is invariably very convex. Metaterga clothed with a cerotegumental crust, usually with 2-4 transverse rows of tubercles/bosses, sometimes with mid-dorsal projections. Pore formula usually normal, porosteles sometimes present. Tergal pubescence often with bisegmented setae. Walking leg coxae mostly contiguous medially, due to very narrow sterna. Head usually slightly transverse, only rarely elongated; antennae usually stout, antennomere 6 usually longest.

Only six recognizable genera are contained in this small family.

Genus *Prosopodesmus* Silvestri, 1910

Type species: *Prosopodesmus jacobsoni* Silvestri, 1910, by original designation (type locality: Batavia (= Jakarta), Java, Indonesia).

= *Homodesmus* Chamberlin, 1918. Type species: *Homodesmus parvus* Chamberlin, 1918, by original designation. Synonymized by Loomis (1950).

= *Rhipidopeltis* Miyosi, 1958. Type species: *Rhipidopeltis sinuata* Miyosi, 1958, by original designation, n. syn.

Diagnosis. Body with 20 segments, pyrgodesmid-like, not capable of volvation, with rather well developed and declivous paraterga. Metaterga with three transverse rows of bosses/tubercles. Gonopods strongly resembling those of typical Polydesmidae, being rather simple, unciform; coxae with only a few ventrolateral setae; telopodites sometimes with a lateral outgrowth at midway, always devoid of a separate solenomere branch; seminal groove terminating distally or apically, hairpad often present.

Genus *Cylindrodesmus* Pocock, 1889

Type species: *Cylindrodesmus hirsutus* Pocock, 1889, by monotypy (type locality: Christmas Island, Australia).

= *Haplosoma* Verhoeff, 1894. Type species: *Haplosoma strubelli* Verhoeff, 1894, by monotypy. Synonymized by Pocock (1898).

= *Haplosomum* Brölemann, 1895. Type species: *Haplosoma strubelli* Verhoeff, 1894. Junior objective synonym of *Haplosoma* Verhoeff, 1894, adopted to eliminate homonymy (Jeekel 1971; Hoffman 1999).

= *Haplodesmus* Cook *in* Cook & Collins, 1895. Type species: *Haplosoma strubelli* Verhoeff, 1894. Junior objective synonym of *Haplosoma* Verhoeff, 1894, adopted to eliminate homonymy (Jeekel 1971).

= *Haplosomides* Attems, 1903. Type species: *Haplosomides moelleri* Attems, 1903, by monotypy. Synonymized by Attems (1907).

= *Lasiodesmus* Silvestri, 1908. Type species: *Lasiodesmus caraibicus* Silvestri, 1908, by monotypy. Synonymized by Loomis (1934).
= *Inodesmus* sensu Loomis 1934, non Cook 1896 (see Golovatch et al. 2001 and above).
= *Elatosus* Chamberlin, 1945. Type species: *Elatosus pygmaeus* Chamberlin, 1945, by original designation. Synonymized by Hoffman (1980) and confirmed by Golovatch et al. (2001).
= *Hypsoporus* Loomis, 1969. Type species: *Inodesmus globulosus* Loomis, 1964, by original designation. Synonymized by Enghoff (1978).

Diagnosis. Body with 19 (♂) or 20 (♀) segments, subcylindrical, not capable of volvation, with paraterga 2 rather well developed, but following ones mostly represented by lateral swellings. Collum and metaterga with abundant setation in part mixed with long, bisegmented, tactile setae. Gonopods especially simple; coxae with only a few ventrolateral setae; telopodite (= solenomere) sometimes with a lateral outgrowth at midway; seminal groove terminating subapically and devoid of a hairpad.

Genus *Helodesmus* Cook, 1896

Type species: *Helodesmus porosus* Cook, 1896, by monotypy (type locality: Java, Indonesia).
= *Gonomastis* Attems, 1930. Type species: *Gonomastis parvula* Attems, 1930, by original designation. Synonymized by Hoffman (1964).
= *Porauxus* Chamberlin, 1945. Type species: *Porauxus pangrangus* Chamberlin, 1945, by original designation. Synonymized by Hoffman (1964).

Diagnosis. Body with 19 segments, subcylindrical, not capable of volvation, with paraterga 2 rather well developed, but subsequent ones mostly represented by lateral swellings. Collum still large, covering the head from above, with 4-5 transverse rows of setigerous tubercles or pits. Following paraterga with three rows of similar tubercles or pits. Pore formula: 5, 7-17(18). Gonopods with poorly setose gonocoxae and a considerably shortened prefemoral+femoral (= setose) part, deeply biramous thereafter, with a long and flagelliform solenomere devoid of a hairpad.

Genus *Atopogonus* Carl, 1926

Type species: *Atopogonus baccatus* Carl, 1926, by monotypy (type locality: New Caledonia, France).

Diagnosis. Body with 20 segments, subcylindrical, not capable of volvation, with paraterga 2 rather well developed, but subsequent ones represented by lateral swellings at

most. Collum small; collum and following paraterga microtuberculate or granular. Gonopods with small virtually bare and reduced gonocoxae and peculiar, strongly geniculate telopodite, coupled with no traces of either a coxal cannula or a seminal groove.

Genus *Doratodesmus* Cook *in* Cook & Collins, 1895

Type species: *Doratonotus armatus* Pocock, 1894. Proposed to replace the preoccupied *Doratonotus* Pocock, 1894 (Cook *in* Cook & Collins 1895) (type locality: Java, Indonesia).

= *Hoplitesmus* Chamberlin, 1945. Type species: *Hoplitesmus enoplus* Chamberlin, 1945. Synonymized by Jeekel (1955).

= *Pauroplus* Chamberlin, 1945. Type species: *Pauroplus analdes* Chamberlin, 1945, n. syn.

= *Eucondylodesmus* Miyosi, 1956. Type species: *Eucondylodesmus elegans* Miyosi, 1956, n. syn.

= *Scolopopyge* Hoffman, 1978. Type species: *Scolopopyge pholeter* Hoffman, 1978, n. syn.

= *Selminarchus* Hoffman, 1978. Type species: *Selminarchus hispidus* Hoffman, 1978, n. syn.

= *Crenatidorsus* Zhang *in* Zhang & Wang, 1993. Type species: *Crenatidorsus grandifoliatus* Zhang *in* Zhang & Wang, 1993, n. syn.

Diagnosis. Body "doratodesmid", with or without mid-dorsal projections; conglobation complete. Gonopod coxae usually abundantly setose ventrolaterally; telopodite usually stout and strongly enlarged laterally towards end of femorite, with or without a short solenomere branch thereafter; acropodite variable, from absent to well-developed.

Genus *Eutrichodesmus* Silvestri, 1910

Type species: *Eutrichodesmus demangei* Silvestri, 1910, by original designation (type locality: Phu-Ly, Vietnam).

= *Dimorphodesmus* Murakami, 1966. Type species: *Dimorphodesmus peculiaris* Murakami, 1966, n. syn.

= *Ascetophacus* Hoffman, 1977. Type species: *Ascetophacus macclurei* Hoffman, 1977, n. syn.

= *Cerastelachys* Hoffman, 1977. Type species: *Doratonotus cavernicola* Sinclair, 1901, n. syn.

= *Dyomerothrix* Hoffman, 1982. Type species: *Dyomerothrix gremialis* Hoffman, 1982, n. syn.

= *Parapauroplus* Zhang *in* Zhang & Wang, 1993. Type species: *Parapauroplus monodentus* Zhang *in* Zhang & Wang, 1993, n. syn.

= *Pocillidorsus* Zhang *in* Zhang & Wang, 1993. Type species: *Pocillidorsus dorsiangulatus* Zhang *in* Zhang & Wang, 1993, n. syn.

Diagnosis. Body "doratodesmid", with or without mid-dorsal projections; conglobation usually complete. Gonopod coxae usually abundantly setose ventrolaterally; telopodite usually slender, not enlarged towards end of femorite, but with a more or less distinct process or outgrowth laterally, opposite recurvature point of seminal groove; solenomere thereafter taking up most of telopodite, sometimes elaborate; seminal groove terminating distally to subapically, with or without a hairpad; acropodite small to nearly absent.

A key to recognizable genera and species of Haplodesmidae:

1 Body with 20 segments, pyrgodesmid-like (collum flabellate, covering the head from above; metaterga with three transverse rows of tubercles; paraterga well-developed, strongly declivous, porosteles often present), incapable of volvation. Gonopods rather simple, unciform; coxae with only a few ventrolateral setae; telopodites basically uniramous, only sometimes with an inconspicuous, lateral outgrowth at midway, always devoid of a separate solenomere branch; seminal groove terminating distally or apically, hairpad often present (*Prosopodesmus*) **2**

– Body with 18, 19 or 20 segments, vermiform (without clear paraterga on most body segments, i.e. incapable of volvation) or "doratodesmid" (with very evident paraterga, mostly capable of tight volvation). Gonopods either simplified (= regressed) or more elaborate, often bi- or triramous **4**

2 Gonopod telopodite with a seminal groove terminating with a hairpad distally (i.e. acropodite rather large, slightly dentate) **3**

– Gonopod telopodite with a seminal groove terminating apically, devoid of hairpad (i.e. acropodite virtually absent) ..... ***Prosopodesmus sinuatus***

3 Gonopod telopodite with a distinct lateral outgrowth at about midway; ozopores absent from paraterga 6 ..... ***Prosopodesmus jacobsoni***

– Gonopod telopodite devoid of a lateral outgrowth at midway; ozopores present on porosteles on paraterga 6 ..... ***Prosopodesmus panporus***

4 Body subcylindrical, not capable of volvation, with paraterga 2 rather well developed, but subsequent ones represented mostly by lateral swellings. Gonopods simplified **5**

– Body "doratodesmid", mostly capable of complete conglobation, with paraterga 2 always very strongly enlarged laterally, all following paraterga more or less strongly declivous while collum somewhat reduced. Gonopods usually rather elaborate **10**

5 Body with 19 (♂) or 20 (♀) segments, collum and all following metaterga with abundant setation in part represented by long, bisegmented, tactile setae. Gonopods especially simple; telopodite = solenomere sometimes with

a lateral outgrowth at midway; seminal groove terminating subapically and devoid of hairpad (*Cylindrodesmus*) **6**

– Body with 19 or 20 segments regardless of sex, collum and all following metaterga without abundant setation, usually tuberculate. Gonopods aberrant 7

6 Gonopod telopodite virtually uniramous ..... ***Cylindrodesmus hirsutus***

– Gonopod telopodite evidently biramous in distal half..... ..... ***Cylindrodesmus villosus***

7 Body with 19 segments, paraterga 2 rather well developed, but subsequent ones mostly represented by lateral swellings. Collum still large, covering the head from above, with 4-5 transverse rows of setigerous tubercles or pits. Following paraterga with three rows of similar tubercles or pits. Gonopods with poorly setose gonocoxae and a considerably shortened prefemoral+femoral (= setose) part, deeply biramous thereafter, with a long and flagelliform solenomere devoid of hairpad (*Helodesmus*) **8**

– Body with 20 segments, paraterga 2 rather well developed, subsequent ones represented by lateral swellings at most; tergal trichome wanting. Collum small. Gonopod coxae virtually bare and reduced; telopodites strongly geniculate and with no traces of either a coxal cannula or a seminal groove (*Atopogonus*)..... **9**

8 Metaterga behind collum with three transverse rows of short setae borne on small tubercles. Gonopod acropodite a long and simple branch. Java..... .....***Helodesmus porosus***

– Metaterga behind collum with three transverse rows of short setae in microsetose pits. Gonopod acropodite a long and bifid branch. Sumatra ....***Helodesmus parvulus***

9 Gonopod acropodite deeply and evidently biramous, apex finely fringed in part..... ***Atopogonus baccatus***

– Gonopod acropodite compact, vaguely biramous, apex not fringed ....***Atopogonus bucculatus***

10 Gonopod telopodite usually stout and strongly enlarged laterally towards end of femorite (Figs 29B, C), with or without a short solenomere branch thereafter; acropodite varying from absent to well-developed (*Doratodesmus*).... **11**

– Gonopod telopodite usually slender, not enlarged towards the end of femorite, but with a more or less distinct process or outgrowth laterally (Figs 4B, C), opposite recurvature point of seminal groove; solenomere thereafter taking up most of telopodite, sometimes elaborate; seminal groove terminating distally to subapically, with or without a hairpad; acropodite small to nearly absent (*Eutrichodesmus*)..... **16**

11 Some metaterga with very evident mid-dorsal processes or outgrowths **12**

– Metaterga without mid-dorsal outgrowths **13**

12 Metaterga 4-19 with a mid-dorsal subtriangular process, gradually increasing in size towards (to become largest on) metatergum 18. Java .... ***Doratodesmus armatus***

– Metaterga before 15th and after 18th (penultimate) without mid-dorsal outgrowths; metaterga 15 and 16 each with a small subtriangular process, metatergum 17 with a particularly prominent, rounded, central process. Sumatra ..... ***Doratodesmus analdes***

13 Most metaterga with 2-3 transverse rows of flat bosses. Gonopod telopodite very simple, femorite very short and stout (much like in *Helodesmus*). New Guinea..... **14**

– Most metaterga with three transverse rows of distinct conical tubercles. Gonopod telopodite more elaborate (Figs 29B, C)..... **15**

14 Male with 18, female with 19 body segments. Gonopod femorite very stout, divided apically into a short, subunciform solenomere and a simple, knife-shaped acropodite ..... ***Doratodesmus pholeter***

– Both sexes with 18 body segments. Gonopod femorite turning apically into a rather short, subunciform solenomere, acropodite wanting..... ***Doratodesmus hispidus***

15 Body with 20 segments. Metatergal tuberculation less distinct, mostly like three transverse rows of bosses (Figs 26A-C). Solenomere branch very short, acropodite rather short and simple (Figs 29B, C). China ..... ***Doratodesmus grandifoliatus***

– Body with 19 segments. Metatergal tubercles also mostly arranged in three transverse rows, but very distinct, conical. Solenomere branch absent, acropodite very long, falcate and conspicuously spinose. Japan..... ***Doratodesmus elegans***

16 Body with 20 segments. At least some metaterga with an evident mid-dorsal outgrowth or projection (Figs 5A, C)..... **17**

– Body with 19 or 20 segments. All metaterga subequal, devoid of an evident mid-dorsal outgrowth or projection (Figs 1A; 22A) **22**

17 Only last 3-8 metaterga in front of telson with an evident mid-dorsal outgrowth (Figs 5A, C) **18**

– Most metaterga, including some of anterior body portion, with a high, often tuberculated projection..... **20**

18 Metaterga 12-19 each with an increasingly evident, subtriangular, mid-dorsal outgrowth. Cave in Yunnan Province, China ... *Eutrichodesmus dorsiangulatus*

– Only metaterga 16(17)–19 each with an evident, rather rounded, mid-dorsal outgrowth..... **19**

19 Paraterga narrower (Fig. 6B). Gonopod process dp much shorter (Figs 7; 8). North Vietnam ..... ***Eutrichodesmus armatocaudatus* sp. n.**

– Paraterga broader. Gonopod process dp much longer. Cave in Yunnan Province, China ..... ***Eutrichodesmus monodentus***

20 Mid-dorsal projections increasingly evident on metaterga 3-18, abruptly smaller on metatergum 19. Distal half of gonopod telopodite enlarged, lobuliform, fringed apically..... ***Eutrichodesmus cavernicola***

– Mid-dorsal projections especially prominent, present on metaterga 5-19, only slightly less prominent on metatergum 19. Male, when known (*E. macclurei*), with distal half of gonopod telopodite slender.....**21**

21 Mid-dorsal projections on metaterga 5 and 6 straight in lateral view..... .....***Eutrichodesmus macclurei***

– Mid-dorsal projections on metaterga 5 and 6 slightly inclined anteriorly in lateral view..... ***Eutrichodesmus reclinatus***

22 Body with 19 segments. Collum and metaterga very densely setose, setae long, bisegmented and tactile (Figs 9; 12A-C). Gonopod telopodite with a highly peculiar dp (Fig. 13)..... ***Eutrichodesmus communicans* sp. n.**

– Body with 20 segments. Collum and metaterga without dense setation. Gonopod telopodite with a different dp.....**23**

23 Most paraterga very wide and only slightly declivous (Figs 14A-D; 15C; 18; 19D). Caves in Guangxi Province, China **24**

– Paraterga not so wide, strongly declivous (Figs 1; 2D; 22C; 23E) **25**

24 Collum with a conspicuous row of teeth all along fore margin of collum (Figs 18D; 19A). Gonopods as in Figs 20C, D; 21 ...***Eutrichodesmus similis* sp. n.**

– Collum without such conspicuous teeth at fore margin of collum (Figs 15A, B). Gonopods as in Figs 16B-E; 17B, C.....***Eutrichodesmus latus* sp. n.**

25 Most metaterga with two transverse rows of bosses. Epiproct very strongly flattened dorsoventrally, subquadrate-spatuliform, with unincised margins. Gonopod telopodite particularly slender, about twice as long as coxa. Japan..... .....***Eutrichodesmus peculiaris***

– Most metaterga with three transverse rows of bosses or conical tubercles. Epiproct never strongly flattened. Gonopods telopodite shorter **26**

26 Paraterga mostly set off laterally at base by a deep sulcus, metaterga with conical tubercles. Gonopod telopodite with a particularly small, dentiform dp.... .....***Eutrichodesmus gremialis***

– Paraterga not set off laterally at base, continuing general outline of metaterga. Gonopod telopodite with a larger and longer dp.....**27**

27 Body up to 5.0 mm long. Paraterga relatively narrow (Figs 1; 2D), volvation imperfect. Gonopods relatively simple (Figs 4B, C) .....***Eutrichodesmus basalis* sp. n.**

– Body at least 7.0 mm long. Paraterga broader (Figs 22; 23E), volvation complete. Gonopods more elaborate **28**

28 Caudolateral and lateral lobulations on most of metaterga deeply incised (Fig. 22). Gonopods with a peculiar, long, biramous, multituberculate dp (Figs 25; 26B, C).....*Eutrichodesmus incisus* sp. n.

– Metaterga not incised caudolaterally. Process dp on gonopods shorter, simple, unciform and pointed.....**29**

29 Body *ca* 8.0 mm long. Gonopod tip bifid. Vietnam..... .....***Eutrichodesmus demangei***

– Body *ca* 14.0 mm long. Gonopod tip simple, unciform. Cave in Yunnan Province, China ..... ***Eutrichodesmus arcicollaris***

Conclusion

There seem to be almost no coherent patterns in the distribution of the various non-genitalic and gonopodial characters in Haplodesmidae. The same concerns geographic distributions. Only very few species pairs can be distinguished in the presently relatively large genera *Doratodesmus* (e.g. *D. pholeter* and *D. hispidus*) and *Eutrichodesmus* (e.g. *E. macclurei* and *E. reclinatus*; *E. latus* sp. n. and *E. similis* sp. n.; *E. demangei* and *E. arcicollaris*). Hence, the discrimination of species groups would be premature at this stage, particularly since many more species of Haplodesmidae can be expected to occur in at least East and Southeast Asia, where the family seems to be centred, as well as in Australasia.

Although most of the haplodesmid species have been described from cave material alone, it is unlikely that this indicates obligate cavernicoly of the group. Most of the caves are simply better explored than the adjacent epigean habitats. Among the known haplodesmids, only very few, particularly those with soft integuments (e.g. *Eutrichodesmus gremialis* and *E. cavernicola*), could be considered as troglobites (Hoffman 1982a), but even this is speculative.

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